Habitat loss and exotic plant invasions disrupt plant–animal mutualisms in a heterogeneous South African landscape

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"*The thing the ecologically illiterate don't realize about an ecosystem is that it's a system. A system! A system maintains a certain fluid stability that can be destroyed by a misstep in just one niche. A system has order, a flowing from point to point. If something dams that flow, order collapses. The untrained might miss that collapse until too late. That's why the highest function of ecology is the understanding of consequences."*

(Frank Herbert, *Dune* [1984]: *Appendix I: The Ecology of Dune*)

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1 General introduction

Biodiversity and global change

We are living on a human-dominated planet (Vitousek et al. 1997). The unprecedented growth of the human population, economic and industrial development, and ongoing globalization are causing major alterations of the Earth system, which are now widely referred to as 'global change' (Vitousek et al. 1997; MEA 2005). The effects of global change on earth's biodiversity are dramatic, and in the past 50 years humanity has more profoundly altered patterns in biodiversity than at any other time in its history (MEA 2005). Amongst others, major drivers of global change that impact on biodiversity are increasing levels of atmospheric CO_2, intensification of land-use, increasing deposition of anthropogenically fixed nitrogen, loss of natural habitats, biotic invasions and climate change (Chapin et al. 2000; Tylianakis et al. 2008). The impacts of virtually all of these drivers are expected to increase in the next 100 years, and dramatic consequences for biodiversity are predicted (Sala et al. 2000; Tylianakis et al. 2008). The implications are of high ecological and social significance, as biodiversity is directly linked to ecosystem functioning and provides essential ecosystem services to humans (Costanza et al. 1997; Hooper et al. 2005). Examples of these services are climate regulation, pest control, nutrient cycling, crop pollination, soil formation and the provisioning of clean air, water and food resources (Myers 1996; Costanza et al. 1997). Understanding how global change affects ecosystem processes that are related to ecosystem functioning and services is thus of growing importance.

Pollination and seed dispersal in a changing world

Species interactions form the template for many ecosystem functions and services. Particularly reciprocally beneficial, i.e. mutualistic, interactions between co-occurring species substantially contribute to the persistence and stability of ecosystems and associated services (Bascompte and Jordano 2007; Thébault and Fontaine 2010). Two of the most prominent mutualisms are pollination and seed dispersal of plants by animals. The global proportion of angiosperms pollinated by animals has been estimated at about 88%, with an even higher proportion in tropical regions (Ollerton et al. 2011). Similarly, the dependence of plants on animals as dispersal vectors is especially high in subtropical and tropical regions, where up to 90% of woody plant taxa depend on seed dispersal by animals (Howe and Smallwood 1982; Jordano 2000). Apart from maintaining ecosystem functioning, both pollination and seed dispersal by animals contribute to important

ecosystem services, such as crop pollination or the maintenance of plant diversity and associated resources in forest ecosystems (Sekercioglu 2006; Klein et al. 2007).

Global change severely affects patterns in species interactions, and mutualisms are no exception (Tylianakis et al. 2008). For pollination, parallel declines of pollinators and dependent plants have been reported (Biesmeijer et al. 2006). Furthermore, ongoing declines in wild pollinator and feral honeybee populations have given indication of a growing 'pollination crisis' (Kearns et al. 1998; Kremen et al. 2002), although the ubiquity of such a crisis has been questioned (Ghazoul 2005). The intensification of land-use, climate change, biotic invasions and ongoing losses in natural habitats and resources are likely to play a major role in explaining declining pollinator populations (Potts et al. 2010).

Similar negative trends have been reported for seed dispersers. Particularly frugivorous animals in subtropical and tropical regions are increasingly under pressure from direct hunting or the loss of natural habitats and resources following deforestation (Sodhi et al. 2004). Generally, the plant–seed disperser mutualism has been described as relatively loose and unspecialized (Herrera 1984), implying an overall high redundancy in the dispersal services provided by different frugivores. Nevertheless, the loss of functionally complementary and specialized dispersers (e.g. large frugivores) may imperil the dispersal of dependent plant species (e.g. plants with large seeds) and thus modify patterns in forest regeneration (Terborgh et al. 2008; Wotton and Kelly 2011).

Habitat loss and plant invasions threaten plant reproductive mutualisms

As outlined above, two of the most detrimental drivers of global change that negatively affect pollination and seed dispersal by animals are the loss of natural habitats and biotic invasions (Potts et al. 2010; Farwig and Berens 2012). Natural habitat loss can endanger and modify plant–pollinator and plant–disperser interactions via the loss and fragmentation of suitable (micro)habitats or changes in habitat and resource conditions (Sodhi et al. 2004; Potts et al. 2010). Correspondingly, numerous studies have shown decreased species richness and lower visitation rates of pollinators and seed dispersers with loss of natural habitat (e.g. Kremen et al. 2002; Kirika et al. 2008; Montero-Castaño and Vilà 2012 and refernces therein). However, in some cases habitat loss or disturbance has been shown to increase pollinator or seed disperser visitation rates and richness on plant species (Farwig et al. 2006; Winfree et al. 2007; Hagen and Kraemer 2010).

Likewise to natural habitat loss, biotic invasions, and here specifically exotic plant invasions often have negative effects on native plant–animal mutualistic interactions. Disruptions of these native interactions may occur directly via competition with native plant species for animal mutualists, or indirectly via shifts in resource composition or in the foraging behavior of consumers (Traveset and Richardson 2006). Exotic plant invasions thus often lead to a reduction in visitation rates or species richness of pollinators or seed dispersers on native plant species (Vilà and D'Antonio 1998; Traveset and Richardson 2006; Dietzsch et al. 2011; Montero-Castaño and Vilà 2012). However, exotic plant invasions can also have neutral or even positive effects on native plant–pollinator or native plant–seed disperser interactions (Moragues and Traveset 2005; Bartomeus et al. 2008; Gleditsch and Carlo 2011).

The great variation in the findings of different studies on changes in pollination and seed dispersal processes with habitat loss or plant invasions may be the result of a general focus on single or few plant species as model species (e.g. Moragues and Traveset 2005; Farwig et al. 2006; Bartomeus et al. 2010; Breitbach et al. 2012). However, results from model species may not be representative for the effects occurring on the scale of the whole interacting plant–animal community. A community approach to the study of pollination or seed dispersal processes thus may allow for more realistic predictions on the effects of natural habitat loss and exotic plant invasions (Farwig and Berens 2012; Herrera and Doblas-Miranda 2013).

Just as community approaches on the effects of natural habitat loss and plant invasion are still largely underrepresented (but see e.g. Albrecht et al. 2013; Chama et al. 2013; Heleno et al. 2013), studies with a focus on multiple drivers of global change are still rare. However, particularly habitat loss and exotic plant invasions are widely believed to exert non-additive, i.e. antagonistic or synergistic, effects on native mutualists and their interactions (Didham et al. 2007; Tylianakis et al. 2008; Potts et al. 2010). The identification of possible interactive effects between habitat loss and plant invasion thus is an important necessary step towards a more holistic understanding of real-world ecosystems.

Quantifying the responses of mutualistic communities to disturbance

Recently, two different statistical tools have received growing attention that improve our understanding of how communities are structured and which drivers act behind these

structures. First, a network approach is increasingly used to investigate patterns in species interactions on a community scale (Bascompte and Jordano 2007). Second, studies increasingly focus on the role of species' functional traits in shaping community composition under changing environmental conditions and shifts in biotic interactions (McGill et al. 2006).

Species interaction networks describe how species of different trophic levels, e.g. plants and animals, directly interact with one another. Links between species of different trophic levels are thereby quantified using the frequency of their interaction in a given time. Interaction frequencies may be quantified as visitation or feeding rates of animals on plant resources, e.g. visitation rates of flower visitors or feeding rates of frugivores. When studying pollination or seed dispersal, one has to keep in mind that visitation or feeding rates do not in all cases reflect effective pollination or seed dispersal (Alarcón 2010; Schupp et al. 2010; King et al. 2013). However, overall, interaction frequencies have been shown to be good estimates of the total effect of animal mutualists on plant species and vice versa (Vázquez et al. 2005; Vázquez et al. 2012). Using quantitative information on interaction frequencies, several metrics that describe the structure of interaction networks have been developed. These metrics measure, for example, the degree of specialization of one trophic level on the other, as well as the overall network specialization (Bascompte et al. 2006; Blüthgen et al. 2006). The use of these specialization metrics may improve our understanding of changes in the structure of mutualistic interactions with disturbance. For example, Aizen et al. (2012) recently showed that plant–pollinator interactions in disturbed habitats are lost non-randomly, with the most specialized interactions disappearing first. Network studies on plant invasions showed that exotic plants often become part of the central core of mutualistic networks, acting as 'supergeneralist' species, with negative effects on native plant–animal mutualisms (Aizen et al. 2008; Vilà et al. 2009; Heleno et al. 2013). However, it is still poorly understood how habitat loss and plant invasions affect plant–pollinator or plant–seed disperser interactions. Furthermore, comparisons between different plant–animal mutualisms have rarely been applied, although such a comparison could hold valuable information on the vulnerability of different mutualisms to habitat loss or plant invasions. Moreover, to my knowledge, no study so far assessed the combined and thus possibly interactive effects of these two drivers of global change on mutualistic interactions on a community scale.

Similar to network approaches, functional trait-based approaches have been increasingly used to understand and predict species' responses to changes in the environment or to changes in community composition (Mouillot et al. 2013). Whether species communities are assembled at random or are structured by external or internal forces such as environmental or competitive filtering (i.e. limiting similarity between ecologically similar species; MacArthur and Levins 1967) has been a long ongoing debate in ecology. Neutral theories commonly assume that species within a trophic level are ecologically identical, and that filtering processes do not play a role for community structure (e.g. Hubbell 2001). In contrast, growing theoretical and empirical work strongly suggests that environmental filtering and competitive interactions among species drive community assembly, and that these structuring forces are mediated by functional traits of species (MacArthur and Levins 1967; Cornwell et al. 2006; Mouillot et al. 2013). Functional traits of species thus may be directly related to species' responses to changing environmental conditions or community composition. Moreover, functional traits of species may strongly determine interactions with species in other trophic levels, and thus influence the structure of interaction networks. For example, plants with deep nectar holders are likely dependent on pollinators with long proboscides for efficient pollination (Stang et al. 2006). Thus, functional traits can also be directly related to species' individual performances under changing conditions (e.g. variation in pollination efficiency of a flower visitor on different plant species; McGill et al. 2006).

The diversity of functional traits and the variation in their distribution in niche space has been termed 'functional diversity' (FD; Schleuter et al. 2010). In many ecosystems, FD within species communities is positively linked to ecosystem functioning and stability (Tilman and Downing 1994; Hooper et al. 2005; Loreau and de Mazancourt 2013). This relationship has been attributed to the different functional roles of species in ecological communities, which can be ecologically redundant or complementary (Díaz and Cabido 2001; Blüthgen and Klein 2011). Consequently, species richness may be a poor representative of the variation in functional traits within communities (Mayfield et al. 2010). So far, it is still poorly understood how the FD within pollinator or seed disperser communities changes with drivers of global change such as natural habitat loss or exotic plant invasions. Focusing on multiple functional traits and environmental gradients is most promising, as the responses of functional traits can differ within the same and among different drivers of habitat disturbance (Cadotte et al. 2011; Spasojevic and Suding 2012).

Again, studies on changes in the FD within species communities will profit from a focus on the effects of multiple drivers on whole plant–animal mutualistic communities (Farwig and Berens 2012).

Outline of the thesis

In the present thesis, I investigated whether natural habitat loss and exotic plant invasions have additive or interactive effects on interactions between plants and their flower visitors and frugivores, and whether these effects differ in their direction and magnitude between the two mutualisms. I used a community approach to assess the overall effects of the two global change drivers on interactions between pollinators and frugivores of native and exotic plants. Specifically, I investigated whether the two drivers induced changes in the interaction structure of plants and their pollinators and frugivores. Further, I investigated whether natural habitat loss and plant invasion cause a loss in pollinator FD, and whether the two drivers cause functional guild-specific changes in the relative importance of frugivore species for frugivory in degraded habitats. With these comprehensive studies on the scale of entire plant–animal communities I aimed at understanding the overall effects of natural habitat loss and exotic plant invasions on the underlying structural properties of communities that determine pollination and seed dispersal of plants (species interactions and FD within communities).

Study area

I conducted my studies in a heterogeneous subtropical landscape, within and around Oribi Gorge Nature Reserve in the province of KwaZulu-Natal, South Africa. The natural vegetation in this heterogeneous landscape is formed by patches of indigenous scarp forest, interspersed by natural grassland. As a consequence of their high degree of biodiversity and endemism, scarp forests are of high conservation priority (Eeley et al. 2001). These forests have a naturally fragmented distribution owing to their biogeographic history as well as to contemporary orographic and microclimatic conditions (Cooper 1985; Lawes 1990). However, because of changes in land-use and increasing urban sprawl, most scarp forests beyond the borders of nature reserves have been heavily reduced in their distribution and extent. In the study region, nowadays only few scarp forest remnants remain within an agricultural matrix, which is primarily constituted by monoculture stands of sugarcane.

In addition to the ongoing loss of natural habitats, exotic plants impose a severe threat to the remaining scarp forests in the region. Particularly at forest edges native plant communities are often replaced by exotic plants such as *Acacia mearnsii* (Mimosaceae), *Ageratum conyzoides* (Asteraceae), *Lantana camara* (Verbenaceae) or *Solanum mauritianum* (Solanaceae). While some non-indigenous plants in the region are still declared casual exotics, many of the most noxious exotic plants have been officially declared invasive species (Henderson 2007). Generally, all of the locally and regionally most abundant exotics contribute to flowering plant communities, and many of these exotics produce fleshy fruits that may attract frugivorous animals. In summary, the presence of two of the most severe threats to the biodiversity in subtropical regions, the loss of natural habitat and exotic plant invasions, made this heterogeneous forest landscape an ideal choice for studying the effects of these two global change drivers on plant–pollinator and plant–frugivore communities.

Objectives

The purpose of this thesis was to investigate the combined effects of natural habitat loss and exotic plant invasions on the structure of plant–pollinator and plant–frugivore interaction networks and the functional composition of pollinator and frugivore communities in a heterogeneous subtropical landscape.

Chapter 2 deals with the structure of plant–pollinator interaction networks along gradients of increasing land-use intensity (i.e. natural habitat loss) and relative abundance of exotic plants. Across 17 study sites that differed in these two gradients, I aimed at understanding whether natural habitat loss and plant invasion had additive or interactive effects on plant–pollinator interactions. I thereby focused on visitation rates of pollinators to native and exotic plants, as well as on the degree of specialization among interacting species. Specifically, I investigated whether specialized interactions were lost and whether pollinator community composition changed towards habitat generalists with increasing natural habitat loss and relative abundance of exotic plants.

Chapter 3 deals with the FD composition of the 17 pollinator communities sampled in the study presented in Chapter 2. Thereby, I investigated whether increasing natural habitat loss and relative exotic plant abundance had additive or interactive effects on the FD of

pollinator assemblages on plant species. I focused on three functional traits that are strongly linked to plant–pollinator interactions and pollination processes: proboscis length, proboscis diameter and body length. I aimed at understanding if there was an overall negative effect of the two drivers on pollinator FD, but also whether effects of the two drivers differed between different functional traits. Further, I included information on species richness of pollinator assemblages to investigate whether changes in pollinator FD on plant species were solely driven by changes in pollinator richness, or whether FD showed divergent patterns.

Chapter 4 reports guild-specific changes in the visitation rates of frugivores to plant species with natural habitat loss and plant invasion. Across nine study sites that differed in their degree of natural habitat loss and relative abundance of invasive plants, I studied whether the responses of frugivores were related to their degree of forest dependency and to their degree of frugivory. Specifically, I investigated whether forest specialists and frugivores with a specialized fruit choice were more negatively affected by additive and synergistic effects between habitat loss and plant invasion than generalist frugivores. Further, I aimed at understanding whether the responses of frugivores to natural habitat loss and exotic plant invasion were linked to the same response traits (forest dependency, degree of frugivory), or if they were trait-specific.

All of the studies in the present thesis have either been published or have been submitted to scientific journals. Thus, these studies represent closed entities that can be read independently of one another. Redundant information among the contents of **chapters 2–4** was therefore in some cases unavoidable.

2 Additive effects of exotic plant abundance and land-use intensity on plant–pollinator interactions

With Dana G. Berens, Franziska Peter & Nina Farwig

A slightly modified version of this chapter
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Abstract

The continuing spread of exotic plants and increasing human land-use are two major drivers of global change threatening ecosystems, species and their interactions. Separate effects of these two drivers on plant–pollinator interactions have been thoroughly studied, but we still lack understanding of combined and potential interactive effects. In a subtropical South African landscape, we studied 17 plant–pollinator networks along two gradients of relative exotic abundance and land-use intensity. Generally, pollinator visitation rates were lower on exotic than on native plants. Surprisingly, while visitation rates on native plants increased with relative exotic abundance and land-use intensity, pollinator visitation on exotic plants decreased along the same gradients. Specialization of plants on pollinators and vice versa decreased with both drivers, regardless of plant origin. Decreases in pollinator specialization thereby seemed to be mediated by a species turnover towards habitat generalists. However, contrary to expectations, we detected no interactive effects between the two drivers. Our results suggest that exotic plants and land-use promote generalist plants and pollinators, while negatively affecting specialized plant–pollinator interactions. Weak integration and high specialization of exotic plants may have prevented interactive effects between exotic plants and land-use. Still, the additive effects of exotic plants and land-use on specialized plant–pollinator interactions would have been overlooked in a single-factor study. We therefore highlight the need to consider multiple drivers of global change in ecological research and conservation management.

Introduction

Biological invasions and increasing human land-use are two major drivers of global change (Didham et al. 2007; Tylianakis et al. 2008). Both lead to a loss in biodiversity and often negatively affect essential species interactions such as pollination (Traveset and Richardson 2006; Tylianakis et al. 2008; Montero-Castaño and Vilà 2012). Most angiosperms and a major proportion of the global crop production depend on biotic pollination (Klein et al. 2007; Ollerton et al. 2011). Thus, understanding the effects of exotic plants and human land-use on plant–pollinator interactions is of critical importance.

Generally, plant invasions lead to competition between exotic and native plants for pollinators (Bjerknes et al. 2007; Morales and Traveset 2009). Competition is especially pronounced if exotic plants act as 'pollination supergeneralists', meaning that their floral resources attract a wide variety of pollinators, leading to high pollinator visitation rates on exotics (e.g. Aizen et al. 2008). Most often, this competition results in decreased pollinator visitation on native plants, which can reduce the reproductive output of native plant species (Dietzsch et al. 2011; Montero-Castaño and Vilà 2012). Yet, the effects of exotic plants on native plant pollination vary considerably among studies, and neutral or even facilitative effects of exotic plants on pollinator visitation to natives have also been reported (Moragues and Traveset 2005; Bartomeus et al. 2010).

Similarly, alteration of natural habitats for human land-use usually negatively affects pollination and plant reproduction (e.g. Aguilar et al. 2006; Potts et al. 2010). Parallel declines of pollinators and insect-pollinated plants have been reported (Biesmeijer et al. 2006), and numerous studies show decreased pollinator richness and abundance in disturbed habitats (e.g. Kremen et al. 2002; Cairns et al. 2005; Potts et al. 2010). However, likewise to the occasionally positive effects of exotic plants, higher land-use intensity can also facilitate pollinator visitation and richness (e.g. Winfree et al. 2007; Hagen and Kraemer 2010).

Both exotic plants and land-use often strongly modify pollinator community composition, which is usually the result of an increase in generalist pollinators and a loss in specialists (Potts et al. 2010). For example, invasive *Rhododendron ponticum* has been shown to decrease the abundance of bumblebees on *Digitalis purpurea*, but to increase visits by flies and syrphids (Dietzsch et al. 2011). Similarly, land-use change from tropical

forest to pasture negatively affects tree-nesting meliponine bees and specialized orchid bees, while promoting the generalist pollinator *Apis mellifera* (Brosi et al. 2008).

Most studies have addressed the effects of exotic plants and land-use on native plant pollination in a separated, single-factor manner, not assessing their combined effects (but see e.g. Bartomeus et al. 2010). However, especially plant invasions and land-use are widely considered to interactively affect native plant–pollinator communities (Didham et al. 2007; Potts et al. 2010). Effects of the drivers may therefore also be non-additive, e.g. antagonistic or synergistic (Sala et al. 2000; Didham et al. 2007). Yet, empirical knowledge is still scarce and far from meeting the needs of conservation management (Didham et al. 2007; Tylianakis et al. 2008). Besides not incorporating other drivers such as land-use, most studies on plant invasion assessed the effects of only a single or few exotic plants on pollination of single or few native plants (but see e.g. Olesen et al. 2002). Results of these studies are not necessarily representative for the effects occurring in the remaining plant community (Morales and Traveset 2009; Williams et al. 2011). Consequently, studying the interactive effects of exotic plants and land-use on entire plant–pollinator communities is a promising approach to understand the complexities arising in real-world ecosystems (Didham et al. 2007; Tylianakis et al. 2008; Montero-Castaño and Vilà 2012).

Plant–pollinator communities are shaped by the interactions among co-occurring species. While pollinator visitation rates lay the basis of these interactions, it is the distribution of species interactions in interaction networks that has been shown to determine community structure (Bascompte and Jordano 2007). In turn, the awareness for conserving species interactions rather than species richness per se is growing (Tylianakis et al. 2010). A network approach is therefore a powerful tool to investigate the consequences of plant invasions and land-use intensity on the structure of plant–pollinator communities (e.g. Aizen et al. 2008; Vilà et al. 2009; Hagen and Kraemer 2010). The sensitivity of species to disturbance may thereby increase with their degree of specialization on their mutualistic partners. Correspondingly, exotic plants or intensified land-use often have the strongest negative effects on specialized native plant–pollinator interactions (e.g. Aizen et al. 2008, 2012; Vilà et al. 2009; Hagen and Kraemer 2010). However, species specialization is still widely measured as species degree (i.e. the number of mutualistic partners with which a species interacts; e.g. Aizen et al. 2012). Yet, these

indices can be strongly influenced by sampling artifacts and overestimate species specialization in rare observations (Blüthgen 2010). A more appropriate alternative are indices that measure specialization as the deviation of observed interactions from a random interaction configuration (Blüthgen et al. 2006). Here, we use such a specialization index to investigate changes in plant and pollinator specialization with increasing exotic plant abundance and land-use intensity. To our knowledge this is the first network approach to the combined effects of these two global change drivers.

In a heterogeneous subtropical landscape in South Africa, we studied plant–pollinator communities and their interactions along gradients of relative exotic abundance and land-use intensity. We expected 1) higher visitation rates on exotic plants than on native plants and 2) decreasing visitation rates on native plants with increasing relative exotic abundance and intensified land-use. We further predicted 3) decreasing specialization of plants on pollinators and vice versa, mediated by 4) a species turnover of pollinators towards generalists with an increase of both global change drivers. Finally, we expected 5) interactive effects between the two drivers on plant–pollinator interactions.

Methods

Study area

We conducted our study in a heterogeneous subtropical landscape within and around Oribi Gorge Nature Reserve (30°S, 30°E, 1,850 ha), near the south coast of KwaZulu-Natal, South Africa. Annual rainfall ranges from 660–1200 mm and annual temperature from 8-28 °C (von Maltitz 2003). The main flowering season starts at the beginning of the rainy season around September. The region's natural vegetation is characterized by indigenous scarp forest. As a consequence of microclimatic and orographic conditions, these forests have a naturally patchy distribution and are often interspersed by natural grassland (Cooper 1985; Lawes 1990). Scarp forests have a high biodiversity and degree of endemism and are therefore of high conservation priority (Eeley et al. 2001). However, particularly at forest edges, exotic plants nowadays dominate many scarp forests, and the distribution and extent of these forests have been drastically reduced by intensification of human land-use (von Maltitz 2003). Consequently, forest remnants outside of protected areas are often heavily invaded and surrounded by an agricultural matrix of sugarcane or timber plantations. Although the honeybee (*Apis mellifera*) is native to South Africa,

managed honeybees may have affected our results. Yet, to our knowledge, and as reported by local landowners and nature conservancies, no beekeeping was conducted in the study area at the time of our study.

Study design

In September 2011, we established 17 study sites, located in forests within and around Oribi Gorge Nature Reserve (see Fig S2.1 and Table S2.1 in the Appendix for a map of the study area and site coordinates). Mean pair-wise distances between study sites ranged from 697 to 21,292 m (8,521 ± 37; mean ± standard error [SE] throughout). In each site, we established one permanent 100 m long and 4 m wide transect situated at forest edges. Forest edges were chosen as they represented centers of exotic plant abundance. Further, establishing all transects at forest edges accounted for edge effects potentially present in small forest remnants but not in continuous forest (Saunders et al. 1991). Still, differences in the effects of the adjacent forest size and the degree of fragmentation surrounding each transect may remain. Transects varied along two gradients: 1) increasing degree of relative exotic plant abundance and 2) increasing degree of human land-use. To assess the degree of relative exotic abundance, we identified all flowering plant species (angiosperms only) every seven to ten days along transects, and recorded their floral abundance in floral units (FU). FU represented the distance between floral entities a medium sized bee would cross flying, rather than walking (Dicks et al. 2002). Plant species and their origin (native or exotic) were identified according to Pooley (1998), Henderson (2007) and Boon (2010). Exotic plants included declared invasive and casual exotic plant species (Richardson et al. 2000a). For each transect, we calculated the mean relative floral abundance of all exotic plants on the total floral abundance over all transect walks, in the following referred to as ‘relative exotic abundance’. To assess the degree of human land-use intensity, we quantified the proportion of natural habitat in a 500 m radius from the center of each transect using ArcInfo GIS 9.3 and a freely available land cover data set (satellite imagery from 2008, 20 m resolution; Ezemvelo KZN Wildlife 2011). Natural habitats included natural forest, natural woodland and bushland as well as natural grassland. We calculated the proportion of all natural habitats on the total area covered by our 500 m radii and defined the degree of land-use intensity as the remaining proportion of non-natural habitat (land-use intensity hereafter). Our land-use intensity index therefore ranges from 0 (no

human land-use) to 1 (no natural habitat remaining). We are aware that the response of pollinators to landscape composition is scale-dependent (Steffan-Dewenter et al. 2002). However, we chose the 500 m radii as we assumed the covered habitat to be used by the majority of pollinators, while more distant habitats might have been only available to some exceptional long-distance foragers (Zurbuchen et al. 2010). Further, our index of land-use intensity in the 500 m radius was highly correlated with land-use intensity in other radii (250–2,000 m), and the choice of the 500 m radius should therefore not substantially affect our results. To ensure that the effects of our two gradients were not confounded, we chose our study sites in such a way that the relative exotic abundance and land-use intensity were only moderately correlated (Pearson correlation: r = -0.51, P = 0.037, n = 17).

Survey of plant–pollinator interactions

We recorded insect flower visitors to flowering plant species (angiosperms only) along transects from September to December 2011. Sampling was conducted between 0900 and 1600 hours and only took place in suitable weather conditions (i.e. no rain, low wind velocity). If possible, we observed all of the plant species flowering along each transect. However, unstable weather conditions and mass flowering in some cases allowed the observation of only the most abundant flowering plant species (see Table S2.3 for completeness of plant observations and the represented plant abundance). The observed plant species richness ranged from 4 to 14 (8.6 ± 0.67) along transects. Observations covered 80 ± 3.0% of all recorded plant species during transect walks, representing 97 ± 1.2% of the total flowering plant abundance. For each focal species, we conducted four observation sessions of 20 min each (80 min × plant species^{-1} × study site^{-1}). We spread observation sessions randomly across transects and plant species during the study period. Insects visiting the reproductive organs of flowers were caught using sweep nets and were stored in 70% ethanol. Flower visitors were assumed to be pollinators. After each session we recorded the number of observed FU and the total abundance of the focal plant species along its respective transect. We identified pollinators to the lowest taxonomic level possible and afterwards sorted pollinator individuals into morphospecies, in the following referred to as species. Insect identification followed Picker et al. (2004), Woodhall (2005) and Scholtz and Holm (2008).

Network analysis

For each study site we compiled a quantitative interaction matrix of the interaction frequencies of the observed plant species and their pollinators, whereby we defined interaction frequency as the number of pollinator visits over the four observation sessions at each plant species (Vázquez et al. 2005). To assess plant specialization on pollinators as well as pollinator specialization on plants we calculated the specialization index *d*' (standardized Kullback-Leibler distance) for each plant and pollinator species per study site, respectively. The index *d*' quantifies the deviation between observed and expected frequency distributions which assume that all species interact with their partners in proportion to their marginal totals (Blüthgen et al. 2006). It is therefore a measurement of interaction exclusiveness and ranges between 0 (highest possible generalization) and 1 (highest possible specialization). We calculated *d*' for each plant species per site, and thus obtained one measurement of specialization on pollinators for each observed plant species per study site (plant specialization hereafter). Similarly, we assessed the specialization of pollinators on plants, calculating pollinator specialization on each plant species in comparison to the full plant community in a given study site. To do so, we first calculated a global *d*' of each pollinator species per study site, that is *d*' was based on all the interactions a pollinator had with all plant species in the respective plant–pollinator network. In a second step, we calculated a weighted mean of the global *d*' of pollinators for each plant species in the network, using the number of observed individuals of the respective pollinators on the plant species as weights. We thus obtained one measurement of specialization of pollinators on plants for each observed plant species per study site (pollinator specialization hereafter). Specialization indices were calculated using the 'bipartite' package (Dormann et al. 2009) in R 2.15.2 (R Development Core Team 2012).

Statistical analysis

Effects on pollinator visitation rate, plant specialization and pollinator specialization

We used linear mixed-effects models to investigate whether pollinator visitation rate differed with relative exotic abundance, land-use intensity and plant origin (native vs. exotic). Relative exotic abundance, land-use intensity and plant origin were treated as fixed effects, while study site was treated as random effect. Further, we standardized pollinator sampling among plant species by including two additional covariates in all

models. First, we included the mean number of observed FU during the four observations sessions on a focal plant species to account for a positive relationship of observed FU and recorded pollinator visits. Second, the attractiveness of a plant species to pollinators may increase with its proportion on the total available resources, i.e. its relative floral abundance on the total floral abundance of all plant species in a given study site. In turn, effects of increasing relative exotic abundance or land-use intensity could differ between plant species with low or high relative abundance. We therefore included information on the relative floral abundance of plant species as a covariate. In a given study site, the relative abundance of a plant species was calculated as the mean floral abundance of all individuals of the plant species flowering at the time of the four observation sessions, divided by the mean total floral display of all species flowering at the time of the observations. Information on the total floral display was taken from floral censuses conducted during the weekly transect walks. Finally, we included three interaction terms in the model. First, to disentangle differences in the responses of native and exotic plants to the two global change drivers, we included the interaction of plant origin with relative exotic abundance and land-use intensity, respectively. Second, to assess synergistic or antagonistic effects of relative exotic abundance and land-use intensity on pollinator visitation rate, we included the interaction of the two global change drivers. The three-way interaction of plant origin, relative exotic abundance and land-use intensity was not significant and therefore eventually omitted from the model. Similarly to the model on pollinator visitation rate, we fitted separate linear mixed-effects models to test the effects of relative exotic abundance, land-use intensity and plant origin and their interactions on plant and pollinator specialization. In contrast to the analysis on pollinator visitation rate, which included the observations on 145 plant species across the 17 study sites (59 different species in total), the analyses on specialization of plants and pollinators included only 131 plant species (53 different species). This reduction was necessary as the specialization index *d'* can only be calculated for species involved in interactions, and therefore not for the remaining plant species which had received no pollinator visits. In all analyses, relative exotic abundance was sqrt-transformed, while number of observed FU and relative abundance of a plant species were log10(x + 1)-transformed. Additionally, we subsequently standardized all continuous response variables to zero mean and unit variance (*z*-transformation) to facilitate the comparison of effect sizes. Linear mixed-

effects models were fitted using restricted maximum likelihood (REML), and Markov Chain Monte Carlo (MCMC; 10,000 iterations) sampling was used to obtain *P*-values of fixed effects (Bolker et al. 2009). In contrast to Wald *t*- or *F*-tests, MCMC sampling does not require the calculation of degrees of freedom (*df*) for random effects. The calculation of *df* in mixed-effects models is still under debate, and MCMC sampling is therefore a more cautious and conservative method for statistical inference (Bolker et al. 2009).

For all the linear mixed-effects models described above, we tested for spatial autocorrelation in the residuals (Moran's *I*) in discrete distance classes of 4000 m (Legendre 1993). We did not detect spatial autocorrelation in any distance class (Moran's *I* close to zero and $P > 0.22$ in all cases), indicating that spatial autocorrelation did not confound the results obtained from mixed-effects models.

Compositional analysis

Pollinator community composition could be affected by ecological factors associated with changes in relative exotic abundance or land-use intensity (e.g. changes in availability of plant resources or nesting sites) but also by spatial effects, like the spatial arrangement of our study sites. To disentangle the contributions of these factors, we were interested in simultaneously assessing these environmental and spatial effects in one multivariate compositional analysis. To identify spatial variables that describe pollinator community composition, we applied a principal coordinates of neighborhood matrices analysis (PCNM) on a Hellinger-transformed plot–pollinator abundance matrix, a suitable transformation for ordination methods and redundancy analysis (RDA; Legendre and Gallagher 2001). PCNM analysis is well suited to detect effects of spatial arrangements and thereby identify spatial eigenvectors which are ordered by decreasing spatial scale (Borcard and Legendre 2002). However, PCNM analysis does not assess the statistical significance of the detected eigenvectors. To select only those eigenvectors which significantly explained pollinator community composition, we used forward selection analysis based on RDA, employing the double-stop criterion (Blanchet et al. 2008). The first stop criterion consists of an adjusted R^2 on a global RDA using all the eigenvectors of the spatial matrix and the pollinator matrix. The second stop-criterion is the α-value set to determine the significance of eigenvectors in a permutation procedure. We set $\alpha = 0.050$, applying 9,999 permutations. We identified one spatial eigenvector, which fulfilled both

stopping criteria (PCNM1: R^2_{adj} = 0.035, P = 0.016). Finally, we used non-metric multidimensional scaling (NMDS) on Bray-Curtis distances of the Hellinger-transformed plot–pollinator matrix, and fitted environmental variables (relative exotic abundance, land-use intensity) and the spatial eigenvector on the two dimensional ordination. The spatial eigenvector was not correlated to relative exotic abundance or land-use intensity ($r < 0.41$; $P > 0.11$; $n = 17$ in both cases), indicating that effects of relative exotic abundance or land-use were independent from spatial arrangement of our study sites. We assessed the significance of the fitted variables by permutation tests (10,000 permutations).

All statistical analyses were carried out with R 2.15.2 (R Development Core Team 2012). We used packages 'lme4' (Bates et al. 2012) for mixed-effects models, 'languageR' (Baayen 2011) to obtain Markov Chain Monte Carlo (MCMC) *P*-values, 'packfor' (Dray et al. 2011) for forward selection and 'vegan' (Oksanen et al. 2012) for PCNM and NMDS analyses.

Results

In 196 h of pollinator sampling, we observed a total of 61 different plant species (145 plant species across the 17 study sites in total; 70 different flowering plant species were recorded during transect walks). Of these, 45 species were native and 14 exotic. The remaining two species could only be identified to genus level and thus were abandoned from all further analyses. Out of the remaining 59 species, we recorded 1,470 interactions between 53 plant (39 native, 14 exotic) and 139 pollinator species (see Tables S2.2+S2.4 for more information on observed plant and pollinator species). Native abundance ranged from 31 to 5,172 FU (1,225 ± 335; mean ± standard error [SE] throughout) while exotic abundance ranged from 0 to 1,553 FU (607 ± 123). The proportion of exotic FU per study site, i.e. relative exotic abundance, ranged from 0.0 to 97% (39 ± 7.3), our index of land-use intensity ranged from 4.0 to 96% (49 ± 6.9).

The plant species with the highest number of pollinator visits were *H. splendidum* (*n* = 234 visits), *Senecio polyanthemoides* (179) and *S. madagascariensis* (131, all native plant species, see Tables S2.2+S2.3 for a list of all recorded plant species during pollinator surveys and transect walks). The exotic plant species with the highest visitation rates were *Lantana camara* (57), *Acacia mearnsii* (45) and *Ageratum conyzoides* (41). The most frequent pollinator was the honeybee (*Apis mellifera*, 367 visits), followed by two

morphospecies in the family Muscidae (127) and Formicidae (60). Overall, we identified 14% of the observed pollinator species to species level, accounting for 30% of all observed individuals (genus: 19% species, 32% individuals; subfamily: 32%, 44%; family: 94%, 95% respectively; Table S2.4).

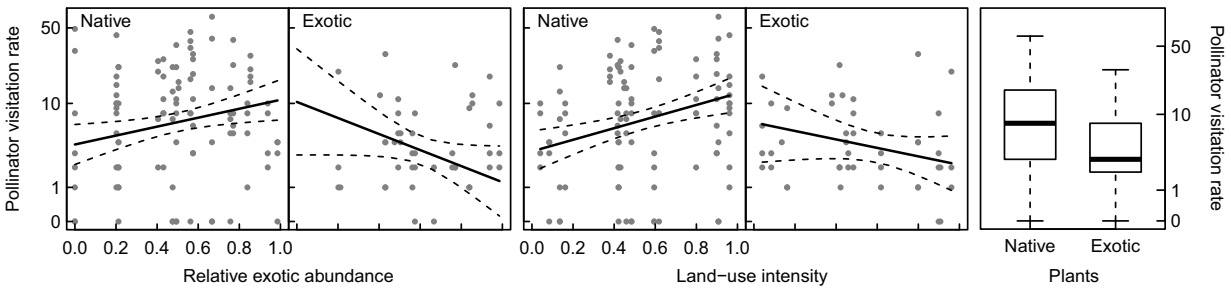

Fig. 2.1 Effect plots of the relationship between pollinator visitation rate on native and exotic plants with increasing relative exotic abundance and land-use intensity in a subtropical South African landscape, as well as boxplot of pollinator visitation rate on native and exotic plants. Effects are based on linear mixed-effects models with relative exotic abundance, land-use intensity and plant origin as fixed effects. Pollinator visitation rates were recorded in 80 min observations of focal plant species (17 study sites). Relative exotic abundance corresponds to the relative abundance of exotic floral display on the total floral display in a given study site. Land-use intensity ranges between 0 (no human land-use) and 1 (no natural habitat remaining) and was measured in a 500 m radius surrounding study sites. Solid lines give effect directions, dashed lines 95% confidence intervals. Grey points show the underlying raw data distribution. Note log10(x + 1) axis for pollinator visitation rate.

After accounting for the number of observed FU and the relative abundance of plant species, pollinator visitation rates on native plant species increased with increasing relative exotic abundance and land-use intensity but decreased on exotic plant species (significant interactions of plant origin x relative exotic abundance and land-use intensity, Table 2.1a; Fig. 2.1). Further, native plants had higher visitation rates (12 ± 1.3) than exotic plants (5.7 ± 0.97; Table 2.1a; Fig. 2.1). Despite changes in pollinator visitation rate along both gradients, we detected no interactive effects of the two global change drivers. The specialization index of plant species decreased with increasing relative exotic abundance and with intensified land-use. These effects did not differ significantly among native or exotic plant species, although there was a marginal trend towards higher specialization of exotic plants with increasing relative exotic abundance (Table 2.1b, Fig. 2.2). Pollinator specialization on plants decreased with increasing relative exotic abundance and

increasing land-use intensity (Table 2.1c; Fig. 2.2). Overall, pollinators had a higher specialization index on exotic plant species than on native plant species (Table 2.1c). As with pollinator visitation rate, relative exotic abundance and land-use intensity did not influence plant or pollinator specialization in an interactive, i.e. synergistic or antagonistic, manner.

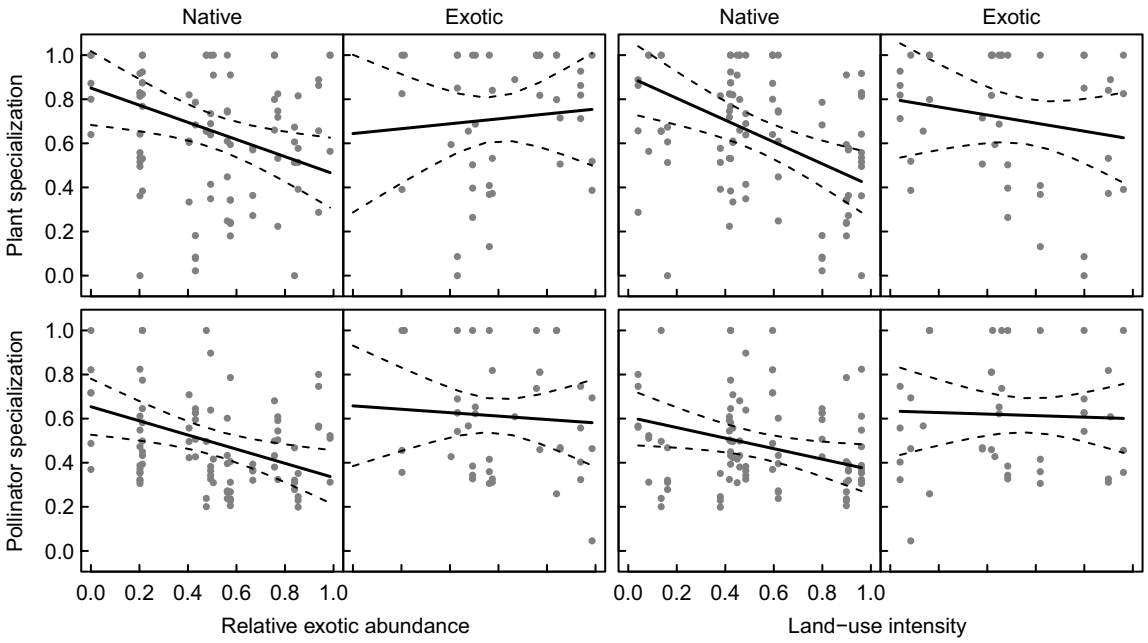

Fig. 2.2 Effect plots of plant and pollinator specialization as a function of increasing relative exotic abundance and land-use intensity for native and exotic plants across 17 study sites in a subtropical South African landscape. Effects are based on linear mixed-effects models, with relative exotic abundance, land-use intensity and plant origin (native vs. invasive) as fixed effects. Solid lines give effect directions, dashed lines 95% confidence intervals. Grey points show the underlying raw data distribution.

Table 2.1 Results from linear mixed-effects models examining the effects of relative exotic abundance, land-use intensity and plant origin (native vs. invasive) on (a) pollinator visitation rate, (b) plant specialization on pollinators and (c) pollinator specialization on plants. The analysis on pollinator visitation rate included observations on 145 plant species across the 17 study sites (59 different species), analyses on specialization of plants and pollinators included only the 131 plant species (53 different species) that received at least one visit. See Methods for calculation of relative exotic abundance and land-use intensity. To standardize observations between plant species, number of observed floral units and relative abundance of a focal plant species on the total plant abundance per site were included. Explanatory variables were standardized to zero mean and unit variance, *P*-values based on Markov Chain Monte Carlo [MCMC]-sampling. Study site was included as random effect in the models.

Source of variation	***Estimate***	***P*[MCMC]**
(a) Pollinator visitation rate		
Floral units observed	0.12	0.0046
Relative abundance plant species	0.16	< 0.001
Plant origin (native vs. invasive)	-0.22	0.0044
Relative exotic abundance	0.11	0.026
Land-use intensity	0.15	0.0028
Plant origin x Relative exotic abundance	-0.30	0.0096
Plant origin x Land-use intensity	-0.26	0.0030
Relative exotic abundance x Land-use intensity	-0.039	0.31
(b) Plant specialization		
Floral units observed	0.013	0.67
Relative abundance plant species	-0.047	0.12
Plant origin (native vs. invasive)	0.064	0.27
Relative exotic abundance	-0.10	0.0086
Land-use intensity	-0.14	0.0010
Plant origin x Relative exotic abundance	0.13	0.097
Plant origin x Land-use intensity	0.090	0.19
Relative exotic abundance x Land-use intensity	0.010	0.83
(c) Pollinator specialization		
Floral units observed	-0.041	0.048
Relative abundance plant species	-0.037	0.15
Plant origin (native vs. invasive)	0.14	< 0.001
Relative exotic abundance	-0.085	0.0046
Land-use intensity	-0.069	0.020
Plant origin x Relative exotic abundance	0.065	0.31
Plant origin x Land-use intensity	0.059	0.26
Relative exotic abundance x Land-use intensity	0.015	0.54

NMDS (stress = 0.16) revealed strong changes in pollinator community composition among study sites (Fig. 2.3). Thereby, both relative exotic abundance and land-use intensity explained a considerable amount in community variation (relative exotic abundance $R^2 = 0.56$; $P = 0.0025$; land-use intensity: $R^2 = 0.45$; $P = 0.015$). In contrast, the explained variation by the spatial eigenvector was lower and not statistically significant ($R^2 = 0.27$; $P = 0.11$), indicating that the spatial arrangement of our study sites only weakly affected pollinator community composition.

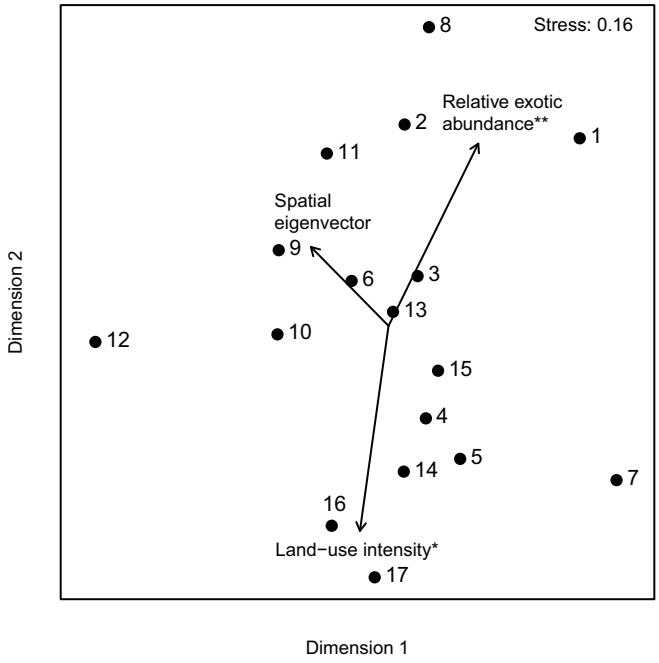

Fig. 2.3 Pollinator community composition across 17 plant–pollinator networks as represented by non-metric multidimensional scaling (NMDS) with two dimensions. Fitted environmental variables include relative exotic abundance ($R^2 = 0.56$; $P = 0.0025$) and land-use intensity ($R^2 = 0.45$; $P = 0.015$), as well as a spatial eigenvector ($R^2 = 0.27$; $P = 0.11$) derived from principal coordinates of neighborhood matrices analysis. Numbers of study sites refer to those used in Fig. S2.1 and Table S2.1, which hold information on the location and characteristics of study sites.

Discussion

Our study shows that both relative exotic abundance and human land-use intensity affected plant–pollinator interactions. Native plants had higher visitation rates than exotic plants. While visitation rates on native plants increased with increasing exotic abundance and land-use, pollinator visits to exotic plants decreased along the two gradients. However, both specialization of plants on pollinators and pollinators on plants decreased with increasing relative exotic abundance and land-use intensity, regardless of plant origin. In line with changes in pollinator specialization, we detected shifts in pollinator community composition along the two gradients, suggesting an increase in generalist pollinators. In contrast to our expectations we detected no interactive effects between the two drivers, and thus all effects of the two drivers seemed solely additive.

Effects of relative exotic abundance and land-use intensity on pollinator visitation rates

Both increasing relative exotic abundance and land-use intensity affected pollinator visitation rates, yet effects differed strongly from our expectations. If the two global change drivers increased the competition between native and exotic plants for pollinator, native plants generally seemed to be the winners. Increasing relative exotic abundance facilitated pollinator visitation to native plants, but led to a decline of visits on exotic plants. Similarly, visitation rates on native plants increased with land-use intensity, while exotics received less pollinator visits. In contrast to our findings, numerous studies report negative effects of exotic plants on pollinator visitation to native plants (e.g. Moragues and Traveset 2005; Dietzsch et al. 2011) and negative effects of increasing land-use intensity on pollinator abundance and richness (e.g. Kremen et al. 2002; Cairns et al. 2005). Several explanations seem plausible to explain these contrasting patterns.

In general, exotic plants received far less pollinator visits than one might expect from studies showing high integration of exotic plants into plant–pollinator networks and describing exotic plants as ‘pollination supergeneralists’ (e.g. Memmott and Waser 2002; Aizen et al. 2008). Further, visitation rates on exotic plants did not increase but even decreased with relative exotic abundance, while visitation rates on natives increased. Higher visitation rates on natives might have been due to a preference of pollinators for native plants. Thus, given a constant abundance of pollinators across study sites, a concentration effect of pollinators on native plant resources at higher relative exotic

abundance might explain the observed pattern. However, it remains speculative why the majority of pollinators did not seem to utilize the abundant exotic plant resources. Differences in floral traits (e.g. floral morphology) between exotic and native species may in some cases explain a reduction in attractiveness or accessibility of exotic floral resources to generalized pollinators (Stang et al. 2006; Morales and Traveset 2009). The most abundant exotic plant species in our study, *Lantana camara* (Verbenaceae), a major driver of relative exotic abundance, strongly differed in its floral morphology from most native plants. The species has a relatively deep corolla, and was mostly visited by butterflies. However, *L. camara* is readily pollinated by honeybees in other areas (Goulson and Derwent 2004), which may indicate that honeybees forage more selectively in their native range as compared to areas where they are also invaders. Moreover, pollinators also rarely visited exotic plants with a floral morphology that indicated generalized pollination syndromes like *Acacia mearnsii* (Mimosaceae) and *Ageratum conyzoides* (Asteraceae). Yet, flowers of some exotic plant species (e.g. *A. mearnsii*) do not produce nectar, which may have forced some pollinators to forage on other plant species (Bernhardt 1987). Finally, some exotic plant species in our study are not yet declared invasive in South Africa, and may be in a lag-phase in which mutualistic interactions are still evolving (Pyšek and Hulme 2005; Henderson 2007). Overall, future studies are needed to clarify the mechanisms behind floral selection between native and exotic plants by pollinators.

Native plants received more pollinator visits with intensified land-use, although landscape alteration usually reduces pollinator abundance (Montero-Castaño and Vilà 2012). Our findings might be due to increasing abundance of generalist pollinators in study sites with high land-use intensity. While habitat specialists may suffer from increasing land-use, habitat generalists can resist increasing land-use intensity to a certain degree (Winfree et al. 2009). Highly mobile and generalized pollinators like the honeybee (*Apis mellifera*) can even outcompete other pollinators and dominate in high land-use habitats (Cairns et al. 2005; Neuschulz et al. 2013). Thereby, pollination of generalist plant species can be maintained (e.g. Neuschulz et al. 2013). Moreover, structurally diverse farmland can provide additional resources and nesting sites not available in natural forests (Hagen and Kraemer 2010). Our results further showed that mainly native plant species seemed to profit from higher pollinator visitation rates with intensified land-use (see also Williams et al. 2011). Exotic plant species like *L. camara* actually received less

visitors, probably due to a reduced abundance of habitat specialists (e.g. butterflies on *L. camara*; Brückmann et al. 2010). However, the widespread dominance of exotic plants in the region suggests that their successful reproduction is not pollinator-limited. For our study system, other plant traits associated with invasiveness, e.g. self-compatibility, high competitiveness for resources and propagule pressure, as well as vegetative spread, may be more important drivers of native plant species decline than competition for pollinators.

Effects of relative exotic abundance and land-use intensity on specialization of plant–pollinator interactions and pollinator community composition

Although exotic plants generally seemed more specialized on pollinators than native plants, increasing exotic abundance increased the amount of generalized plant–pollinator interactions. However, as mentioned above, low visitation rates on exotics despite increasing relative exotic abundance indicated strong preferences of pollinators for native plants. With a reduction in the amount of native plant resources, specialized native plant–pollinator interactions might have been lost (Traveset and Richardson 2006; Aizen et al. 2008). Moreover, pollinators may have altered their foraging behavior (Ghazoul 2004), as increasing relative exotic abundance should prolong the time needed by pollinators to locate the remaining native floral resources. Similarly, competition on native plants should increase. According to optimal foraging theory, both prolonged location time and higher competition could induce a less specialized foraging behavior (MacArthur and Pianka 1966; Fontaine et al. 2008). Changes in the specialization of plant–pollinator interactions with exotic abundance therefore might have been driven directly through a loss of specialized interactions, but also indirectly by changes in the availability of preferred native floral resources.

Likewise to the effects of exotic plants, increasing land-use intensity led to reduced specialization of plant–pollinator interactions. A part of the similar effects might be explained by the moderate correlation of relative exotic abundance and land-use intensity in our study. However, overall the effects of exotic plants and land-use should occur at different spatial scales (e.g. Bartomeus et al. 2010). Moreover, there is strong evidence from studies showing the negative effects of increasing land-use intensity on pollination (e.g. Kremen et al. 2002; Potts et al. 2010; Aizen et al. 2012). Specialized plant–pollinator interactions are particularly prone to be lost with increasing habitat disturbance (e.g. Aizen

et al. 2012). In our study, we measured land-use intensity mainly as the loss of natural forest cover. Thereby, higher land-use intensity reflected a reduction in the amount of natural habitat and possibly increased habitat fragmentation. Both of these factors often reduce the abundance of specialist plants and pollinators (e.g. Aguilar et al. 2006; Brückmann et al. 2010). A loss of specialist plants and pollinators in turn may have promoted an overall generalization of plant pollinator interactions. In line with the lower specialization on plants, we detected a shift in pollinator community composition, indicating a higher abundance of pollinator generalists, such as *A. mellifera*. While dietary specialists may be especially prone to local extinction, disturbance-adapted pollinators such as *A. mellifera* often have an unspecialized foraging strategy (Potts et al. 2010). *Apis mellifera* thus may be an effective pollinator of many generalized plant species. However, depending on a single pollinator species increases risks associated with annual fluctuations and ongoing declines in wild and managed honeybee populations (Potts et al. 2010). Moreover, functional complementarity among pollinator species can enhance pollination efficiency and the stability of plant–pollinator communities (Fontaine et al. 2006; Albrecht et al. 2012). We therefore encourage the preservation of specialized and diverse native pollinator communities to ensure effective pollination of native plants in the future.

Interactive effects of the two global change drivers

Contradictory to our expectations and ecological theory (Didham et al. 2007), we neither detected synergistic nor antagonistic interactive effects between exotic plants and land-use on native or exotic plant–pollinator interactions. Synergistic effects on native plants might have arisen if exotic plants had attracted the majority of pollinators in high land-use habitats. However, exotic plants like *L. camara* did not seem to attract many pollinator species and actually received less pollinator visits with increasing land-use intensity. Weak integration into the local community and overall high specialization of exotics on specific pollinators thus may have prohibited multiplicative negative effects of exotics on native plants in high land-use habitats. We neither detected antagonistic or mitigating effects between exotic plants and land-use, where highly rewarding exotic plants could have attracted pollinators in high land-use intensity areas. This contrasts the findings of Bartomeus et al. (2010), who showed that high floral abundance of exotic *Impatiens glandulifera* diminishes the importance of the surrounding landscape structure by

attracting bumblebees over large distances. However, in their study, Bartomeus et al. (2010) focussed on a single highly abundant and rewarding exotic plant species. In our community-wide study, effects on pollinators may have been idiosyncratic between different exotic plant species. Further, the weak integration of exotic plants may have prevented synergistic or antagonistic interactions with land-use.

Although exotic plants and land-use did not have interactive effects on native plant pollination, both similarly seemed to reduce the abundance of specialized plant–pollinator interactions, which can precede the extinction of specialized plants or pollinators (Aizen et al. 2008, 2012; Tylianakis et al. 2008, 2010). Our study design allowed us to separate the effects of exotic plants and human land-use and revealed that conserving specialized native plant–pollinator interactions and preventing a potential species decline (Pauw and Hawkins 2011) will require tackling the two global change drivers separately. As studies on single driver effects would have overlooked the additive effects we detected in this study, we highlight the need for more studies on additive and non-additive effects of multiple drivers of global change on ecosystem processes on a community scale.

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3 Natural habitat loss and exotic plants reduce the functional diversity of pollinators in a heterogeneous subtropical landscape

With Dana G. Berens, & Nina Farwig

A slightly modified version of this chapter
has been resubmitted to *Functional Ecology*

Abstract

Functional diversity (FD) of pollinators increases plant reproductive output and the stability of plant–pollinator communities. Yet, in times of worldwide pollinator declines, effects of global change on pollinator FD remain poorly understood. Loss of natural habitat and exotic plant invasions are two major drivers of global change that particularly threaten pollinator diversity. In a subtropical South African landscape, we investigated changes in the FD of pollinator assemblages on native and exotic plants along gradients of natural habitat loss and relative abundance of exotic plants. We used a dataset of 1434 pollinator individuals sampled on 131 focal plants and calculated the FD in three pollinator traits that are strongly related to plant–pollinator interactions and pollination processes: proboscis length, proboscis diameter and body length. Multivariate FD of pollinators decreased with both increasing natural habitat loss and relative exotic abundance. Importantly, changes in FD went beyond those in pollinator richness. Furthermore, richness was not related to either natural habitat loss or relative exotic abundance. Loss in multivariate FD seemed to be mediated by complementary negative effects of natural habitat loss on FD in proboscis length and relative exotic abundance on FD in body length, respectively. Correspondingly, we recorded lower abundances of long-tongued pollinators with natural habitat loss and reduced variance in body size with both drivers. In contrast, FD in proboscis diameter was unaffected by either driver. All effects of the two global change drivers were non-interactive. Our results show that both natural habitat loss and exotic plants negatively affect pollinator FD, which may imperil pollination of specialized plant species in degraded habitats. Pollinator richness is a poor representative of pollinator FD and likely insufficient when assessing the consequences of habitat loss or plant invasion on pollination processes. Distinct responses of pollinator traits to the two drivers suggest limited options to infer relations of one trait to another. Finally, additive effects of natural habitat loss and exotic plant invasions highlight the need to consider multiple drivers of global change when investigating ecosystem processes at a community scale.

Introduction

Functional diversity (FD) – the diversity of species' properties that influence their individual performances (McGill et al. 2006; Schleuter et al. 2010) – is an integral part of biodiversity. Species communities with high FD are often more productive and stable (Díaz and Cabido 2001; Loreau and de Mazancourt 2013). For pollinator communities, FD can be the result of interspecific variation in behavioral or morphological traits such as differences in flower handling or the size of mouthparts (Fontaine et al. 2006; Albrecht et al. 2012). Interspecific variation often results in niche partitioning and functional complementarity of pollinators, which increase plant reproductive output and crop yield (Hoehn et al. 2008; Blüthgen and Klein 2011; Albrecht et al. 2012). Variation in functional traits of pollinators thus is likely more important for pollination processes than pollinator richness per se (see Díaz and Cabido 2001 for an example on plants). Studying the FD of pollinator communities along environmental gradients thus is a promising approach to predict consequences of changing environments for the structure and persistence of plant–pollinator communities (McGill et al. 2006; Potts et al. 2010; Williams et al. 2010). A deeper understanding of these processes is particularly important in times of worldwide pollinator declines, which are widely believed to result from human-induced global change (Vitousek et al. 1997; Potts et al. 2010).

Especially plant species within subtropical and tropical forests are highly dependent on animal pollinators for reproduction (Bawa et al. 1985; Ollerton et al. 2011). However, these forests are increasingly under pressure from the loss of natural habitat and invasions by exotic plants (Sala et al. 2000; Chapin et al. 2000). Numerous studies have investigated the effects of these two drivers of global change on plant–pollinator interactions, and effects seem to a large extent to be negative (Montero-Castaño and Vilà 2012 and references therein). Yet, most studies generally focus on pollinator richness and abundance as proxies for changes in the composition of pollinator communities.

In contrast, effects of natural habitat loss and exotic plant invasions on the FD of pollinator communities are poorly understood, although several studies suggest that losses are likely. Overall, simplified agricultural landscapes seem to support less functionally diverse insect communities than do structurally complex natural habitats (e.g. Tscharntke et al. 2008). For pollinators, a loss in FD could result from negative effects of habitat loss on small and immobile species (Greenleaf et al. 2007; Brückmann et al. 2010). Similarly,

the dominance of a single or few exotic plant species could trigger a loss in pollinator FD as the amount and diversity of native floral resources decreases (Traveset and Richardson 2006). Importantly, changes in pollinator FD associated with habitat loss or plant invasion are likely to differ among different investigated functional traits of pollinator species, and multiple assembly processes may neutralize each other (Spasojevic and Suding 2012). Thus both multivariate and univariate measures of FD are needed to disentangle changes in pollinator FD and their underlying mechanisms. Moreover, interactive, i.e. antagonistic or synergistic, effects between habitat loss and plant invasion are generally believed to strongly increase the risk of pollinator and associated native plant species decline (Biesmeijer et al. 2006; Didham et al. 2007; Potts et al. 2010). While not yet empirically studied, synergistic effects of the two drivers thus are a likely threat to the FD of pollinator communities in highly disturbed habitats.

Here we studied the combined effects of natural habitat loss and exotic plants on the FD of pollinator communities in a subtropical South African landscape. We investigated multivariate and univariate FD in three pollinator traits which are strongly related to plant–pollinator interactions and pollination processes: proboscis length, proboscis diameter, and body length (Greenleaf et al. 2007; Stang et al. 2009; Ibanez 2012). We hypothesized a decrease in multivariate pollinator FD with both global change drivers. We expected this decrease to be caused by reductions in univariate FD among the three pollinator traits, with separate responses of individual pollinator traits to the two drivers. Finally, we expected negative synergistic effects between the two drivers on pollinator FD.

Methods

Study area

We conducted our study in a heterogeneous subtropical landscape within and around Oribi Gorge Nature Reserve (30°S, 30°'E; 1,850 ha), near the south coast of KwaZulu-Natal, South Africa. The natural vegetation in the region is characterized by indigenous scarp forests, interspersed by patches of natural grassland (Cooper 1985; Eeley et al. 2001). However, most grassland has been converted into sugar cane fields, and the remaining scarp forests have been drastically reduced in their distribution and extent by the intensification of land-use and urban sprawl (von Maltitz 2003). Furthermore, numerous

exotic plant species are serious pests in the region and scarp forest edges are often heavily invaded by exotic plants such as *Lantana camara* (Verbenaceae), *Acacia mearnsii* (Fabaceae) and *Ageratum conyzoides* (Asteraceae). However, not all scarp forests are invaded to the same degree, regardless of whether they are situated within nature reserves or the agricultural matrix. Consequently, the remaining natural habitat cover and the abundance of exotic plants along scarp forest edges are not generally correlated. Accordingly, we were able to separate the effects of loss of natural habitat and relative exotic plant abundance on pollinator FD in this subtropical landscape.

Study design

In September 2011, we established 17 study sites, located in forests within and around Oribi Gorge Nature Reserve. Mean pair-wise distance between study sites ranged from 697 to 21,292 m (mean ± SD: 8,521 ± 153 m). In each site, we established one permanent 100 m long and 4 m wide transect situated at forest edges. As stated above, forest edges were chosen as they represented centers of exotic plant abundance, but also to assure comparability of intensities of edge effects on pollinator communities across studies. Establishing study sites within forests would have confounded results owing to stronger edge effects in forest remnants than in continuous forest (Saunders et al. 1991).

To quantify natural habitat loss, we estimated the percentage of remaining natural habitat (scarp forests, small patches of remaining grassland) in a 500 m radius surrounding the center of each transect in a given study site, using digital maps and a regional land cover data set (Ezemvelo KZN Wildlife 2011). We expected this radius to be covered by the majority of flying insect pollinators (Greenleaf et al. 2007), yet, natural habitat cover in the 500 m radius was also strongly correlated to the cover in smaller and larger radii (250–2000 m). Loss of natural habitat was then defined as the proportion of the remaining non-natural habitat cover in the 500 m radius. To quantify the proportion of exotic plants on the total plant community in each study site, we performed transect walks every 10–14 days during the field season, and estimated the floral abundance of flowering angiosperm species (in floral units; [Dicks et al. 2002]). We then classified species into natives and exotics, and calculated the mean relative exotic abundance on the total flower display per transect over all transect walks (varying between 0 and 1; i.e. no exotic floral display and only exotic flowers). More detailed information on the methods involved in quantification

of natural habitat loss and relative exotic abundance is provided in a previously published study on the network structure of the studied plant–pollinator communities (Grass et al. 2013).

Origin of data on plant–pollinator interactions

Our dataset was based on recently published data on plant–pollinator communities of our 17 study sites (Grass et al. 2013). In short, pollinator visitation to plants was observed on a total of 70 different plant species flowering across the transects in the 17 sites. As a plant species could also be present in multiple study sites, we observed a total of 145 focal plants. Observations per focal plant consisted of four randomly allocated observation sessions of 20 min each (80 min × focal plant^{-1} × study site^{-1}). All pollinators were identified to the lowest taxonomic level possible and afterwards sorted into morphospecies, hereafter referred to as 'species' (139 pollinator species in total). See Grass et al. (2013) for more information on survey of plant–pollinator interactions, chosen focal plants for pollinator observations and taxonomic resolution of pollinator identification. For this study, we selected a subset of 131 focal plants, where every focal plant had received at least one pollinator visit, covering a total of 1434 pollinator individuals. Note that in the following, we use the terms 'pollinator community' to refer to regionally (study area) and locally (within study sites) present pollinator species, and 'pollinator assemblage' to refer to the specific subset of a local pollinator community on a given focal plant.

Measurement of pollinator functional traits

We measured the proboscis length, proboscis diameter and body length of up to 12 individuals per pollinator species, depending on abundance. All measurements followed the methods described in Stang et al. (2006), except that we did not measure the length of the hind femur (Stang et al. 2006) but of the whole hind leg for calculation of body length. Measurements were undertaken under a dissecting microscope using an ocular micrometer and taken to the nearest 0.1 mm. In total, functional traits of 491 individuals including 131 pollinator species were measured (measurements could not be undertaken for eight species due to damages, yet the 131 measured species represented 98% of all plant–pollinator

interactions in our dataset; Table S3.1 in the Appendix). Correlations among mean values of pollinator traits were weak to moderate (r = 0.16–0.43).

Quantification of functional diversity

Our aim was to understand changes in pollinator FD on plant species in differently disturbed study sites. We thus calculated pollinator FD for each focal plant in a given study site, based on the pollinator assemblage of the plant. We used functional dispersion (FDis) as per Laliberté and Legendre (2010) to quantify the FD of a given pollinator assemblage. Functional dispersion measures the mean distance of species' trait values to the centroid of all species in trait space. The index is relatively unaffected by species richness, weighs trait values by species' abundances and can be calculated for one or multiple traits (Laliberté and Legendre 2010). Information on abundance of pollinator species on a focal plant was derived from the number of visits of the species in 80 min of observations (see Methods above; Grass et al. 2013). We calculated multivariate FDis based on the dispersion of the three traits within the pollinator assemblages on each of the 131 focal plants across our 17 study sites. Similarly, we calculated univariate FDis of each pollinator trait on each plant.

We then used null model analysis to infer whether the observed pollinator FD on a focal plant deviated from a model of random pollinator assembly (Gotelli and Graves 1996; Mouchet et al. 2010). We first created a plant–pollinator interaction matrix of the 131 focal plants and the 131 pollinator species, based on the interaction frequencies of plants and pollinators. Secondly, to gain an expected null distribution of pollinators on plants, we shuffled the entries of this matrix while keeping the marginal sums constant (10,000 randomizations). Thereby, we created random pollinator assemblages on each focal plant per study site from the regional pollinator pool while keeping pollinator abundance per plant and study site constant, yet allowing pollinator composition and richness to vary. With our null model approach we aimed at eliminating potential barriers imposed on pollinator species from the regional species pool that could select for specific pollinator traits in disturbed habitats. Still, we are aware that this approach is limited in so far as it does not include pollinators that were potentially present in the region but not recorded during pollinator sampling (Pärtel et al. 2011; Spasojevic and Suding 2012). We calculated the expected FDis of multivariate and univariate FDis as the mean of their FDis

values over all randomizations, respectively, and then defined functional diversity (FD) as the deviance between observed and expected FDis values as $FD_{trait} = FDis_{trait\_observed} - FDis_{trait\_expected}$ (Spasojevic and Suding 2012). Using the expected FDis values of the 10,000 randomizations, we inferred significant positive (overdispersion) or negative (underdispersion) departure from the null expectation at $\alpha = 0.025$.

Statistical analyses

As we investigated changes in pollinator FD on the level of plants within study sites, our statistical analyses must account for the hierarchical design of our study. We therefore fitted linear mixed-effects models using R package 'lme4' (Bates et al. 2012) with study site as random factor. All models were fitted using restricted maximum likelihood (Bolker et al. 2009).

We generated separate global models for multivariate and univariate FD in pollinator assemblages on focal plants across study sites. In each global model, we included plant origin (native or exotic), natural habitat loss and relative exotic abundance as predictors, as well as the interaction of the two drivers. We excluded the interactions of plant origin and the two drivers, as origin of plants had no effect on changes in pollinator FD with the two drivers. To account for differences in floral abundance of focal plants, we included the relative floral abundance (ln-transformed) of each observed plant on the total floral abundance of all flowering plant species in a given study site (Grass et al. 2013). Here, we used data from vegetation surveys to calculate means of floral abundance of plant species flowering at the time of the four observation sessions in a given study site. Including additional information on the number of observed floral units during surveys of plant–pollinator interactions did not qualitatively affect the results, and was therefore omitted for simplicity. Finally, although our measure of FD is largely unaffected by pollinator richness, we included pollinator richness (log10-transformed) of assemblages on a given focal plant to investigate whether changes in FD went beyond those in pollinator richness. In statistical notation, the full model read as:

1) FD measure ~ log10(pollinator richness) + ln(relative abundance of focal plant) + plant origin + natural habitat loss × relative exotic abundance + (1 | study site)

To discern whether our measures of FD carried different (and thus potentially more ecologically relevant) information than pollinator species richness, we compared our results on changes in pollinator FD to those on an analysis with pollinator richness as response variable (log10-transformed). Model structure was similar to that described above, except for excluding richness as predictor.

In this study, we assumed natural habitat and increasing relative floral abundance of exotic plants to be the main drivers of changes in pollinator FD. However, pollinator FD on a focal plant may not only be affected by habitat loss or exotic plant invasion, but can also be influenced by species-specific effects of the sampled plant species. For example, significantly underdispersed pollinator FD on a given plant could result from habitat degradation, but also from functional constraints imposed by floral traits (e.g. a deep corolla tube; Pauw et al. 2009; Ibanez 2012). These and other co-evolutionary adaptations between plants and their pollinators are often phylogenetically conserved (e.g. Rezende et al. 2007). We therefore conducted a series of statistical analyses to verify that increasing natural habitat loss and exotic plant abundance were the main drivers of changes in pollinator FD (for detailed methods and results see Appendix of chapter 3). Firstly, using permutational MANOVA, we analyzed whether plant composition changed with increasing habitat loss or relative exotic abundance. Secondly, we included information on floral morphology (nectar holder depth, nectar holder width, size of the alighting place) into our mixed-effects models and compared effect sizes of habitat loss and relative exotic abundance to those of models without these covariates. Thirdly, to account for additional phylogenetically conserved traits and overall variation in the phylogenetic structure of plant communities across study sites, we included phylogenetic eigenvectors into our models and again compared effect sizes.

Information on changes in the FD of species communities along environmental gradients is insufficient if there is no indication of the reasons behind these changes (for example a loss in pollinator groups with ‘extreme’ functional traits). Furthermore, even if FD is unaffected, the mean of a functional trait may change with increasing disturbance (with the variance around this mean remaining constant). We therefore quantified the direction of changes in pollinator FD by investigating weighted mean pollinator traits on each focal plant across the 17 study sites. Our approach resembled the calculation of community weighted mean trait values as applied in other studies (e.g. Spasojevic and

Suding 2012). Yet, similar to FD, we calculated the weighted mean of pollinator traits on the level of plant species and not on the level of study sites. The structures of the mixed-effects models were similar to those on FD of pollinators. However, we did not expect pollinator richness or relative abundance of focal plants to affect the weighted mean of pollinator traits, and including this information did not qualitatively affect our results. Consequently, we excluded these covariates from the models. In addition to analyses on weighted means of pollinator traits, we used multivariate analysis to identify the most important pollinator groups driving the observed changes in trait values (detrended correspondence analysis; see Appendix of chapter 3 for detailed methods and results). Here we focused on compositional changes at the taxonomic level of pollinator families to reduce taxonomic complexity and achieve homogeneity in taxonomic resolution across pollinator morphospecies. We fitted natural habitat loss and relative exotic abundance on a two-dimensional ordination and used different coloration to visualize changes in weighted means of functional traits across pollinator families.

For each linear-mixed effects model we tested for spatial autocorrelation in the residuals (Moran's *I*) in discrete distance classes of 4000 m (R package 'spdep'; Bivand et al. 2013). We found no evidence of spatial autocorrelation in any distance class (Moran's *I* close to zero and $P > 0.12$ in all cases). Except for the categorical variable 'plant origin', all predictor variables were *z*-transformed (standardized to zero mean and unit variance) to facilitate the comparison of effect sizes (i.e. estimates of predictors). All statistical analyses were conducted in R 2.15.2 (R Development Core Team 2012).

Results

Multivariate FD of pollinators decreased with both global change drivers, i.e. along our gradients of natural habitat loss and increasing relative exotic plant abundance (Table 3.1; Fig. 3.1). Notably, effects of the two drivers were strong, although pollinator richness was included in the model and generally had a positive effect on pollinator FD (Table 3.1).

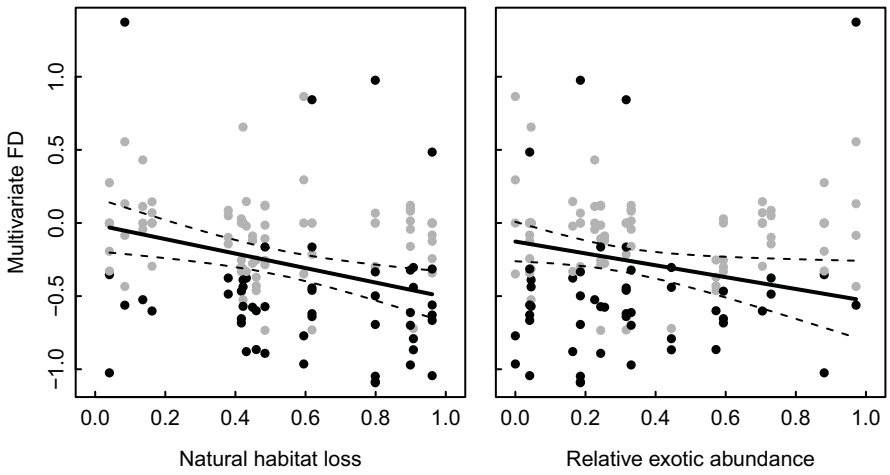

Fig. 3.1 Loss in multivariate FD of pollinators with increasing loss of natural habitat (left panel) and relative abundance of exotic plants (right panel) in a heterogeneous subtropical landscape. Calculation of multivariate FD was based on three pollinator traits (proboscis length, proboscis diameter and body length). Shown are effects of drivers from a linear mixed-effects model (black line) and 95% confidence intervals (dashed lines). Effects are corrected for other covariates in the model. Grey and black points show the underlying raw data for each pollinator assemblage on a given focal plant, with black points indicating significant deviation from null model distribution.

Changes in multivariate FD thereby seemed to be mediated by complementary negative effects of the two drivers on different pollinator traits (Fig. 3.2). FD in proboscis length decreased with natural habitat loss. FD in body length decreased with natural habitat loss and also with increasing relative exotic abundance (Table 3.1; Fig. 3.2). In contrast, natural habitat loss only had a marginal negative effect on FD in proboscis diameter (Table 3.1). Except for FD in proboscis length, FD in the other pollinator traits as well as multivariate FD was always higher on exotic than on native focal plants (Table 3.1). In contrast to our expectation of interactive effects of the two global change drivers, we did not detect a significant interaction of natural habitat loss and relative exotic abundance in any model (Table 3.1). Importantly, in contrast to the observed changes in

FD measures, species richness of pollinators on plants was neither related to increasing natural habitat loss nor relative exotic abundance across study sites (Table S3.2; Fig S3.1).

Table 3.1 Changes in multivariate and univariate functional diversity (FD) of pollinator assemblages on native and exotic plants (131 focal plants) along gradients of loss of natural habitat and of relative exotic plant abundance (17 plant–pollinator communities). Effects were corrected for pollinator richness and the relative floral abundance of a focal plant on the total floral abundance of all flowering plant species in a given study site. Predictors were standardized to zero mean and unit variance to ease the comparison of effect sizes.

	Source of variation	Estimate	*Z*	*P*
Multivariate FD	Pollinator richness	0.10	2.8	0.0054
	Relative abundance	-0.092	-2.5	0.013
	Plant origin	0.23	3.0	0.0028
	Natural habitat loss	-0.14	-3.1	0.0017
	Relative exotic abundance	-0.12	-2.2	0.030
	Natural habitat loss × Relative exotic abundance	-0.055	-1.4	0.17
FD in proboscis length	Pollinator richness	0.0067	0.24	0.81
	Relative abundance	-0.034	-1.2	0.22
	Plant origin	0.067	1.2	0.25
	Natural habitat loss	-0.088	-2.6	0.010
	Relative exotic abundance	-0.049	-1.2	0.22
	Natural habitat loss × Relative exotic abundance	-0.042	-1.4	0.16
FD in proboscis diameter	Pollinator richness	0.075	2.9	0.0035
	Relative abundance	-0.057	-2.3	0.024
	Plant origin	0.19	3.5	< 0.001
	Natural habitat loss	-0.057	-1.8	0.070
	Relative exotic abundance	-0.053	-1.4	0.15
	Natural habitat loss × Relative exotic abundance	-0.019	-0.69	0.49
FD in body length	Pollinator richness	0.054	2.6	0.011
	Relative abundance	-0.047	-2.3	0.025
	Plant origin	0.094	2.1	0.035
	Natural habitat loss	-0.063	-2.4	0.016
	Relative exotic abundance	-0.065	-2.1	0.034
	Natural habitat loss × Relative exotic abundance	-0.021	-0.91	0.36

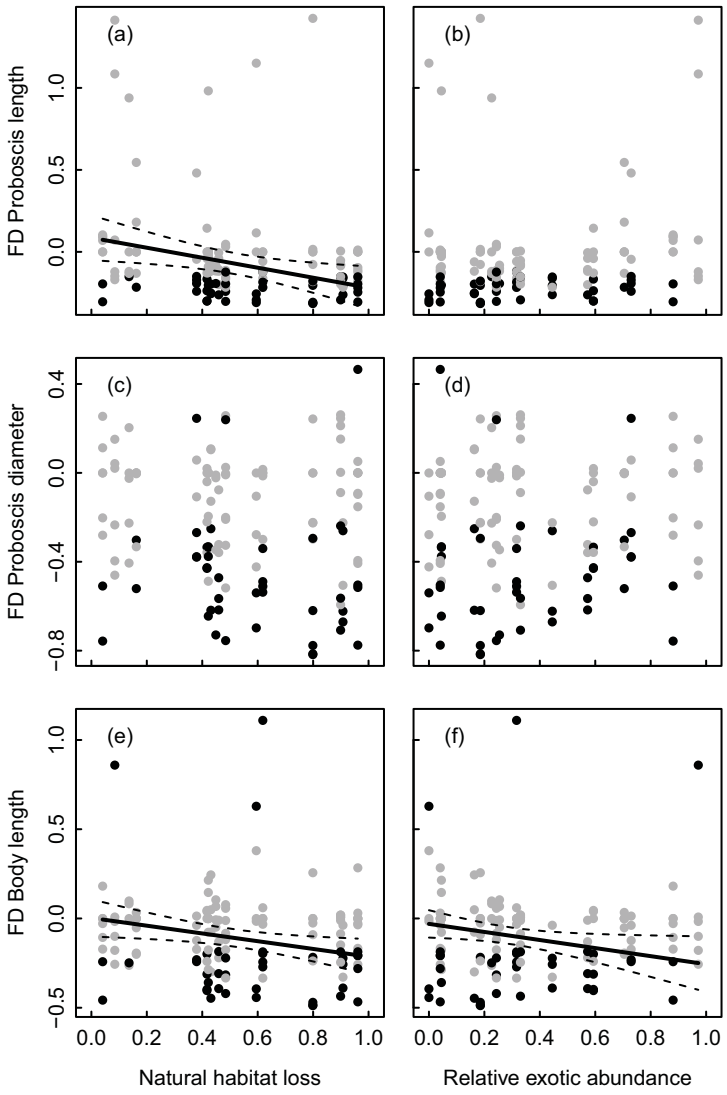

Fig. 3.2 Changes in FD in three pollinator traits with increasing loss of natural habitat and relative exotic plant abundance. Natural habitat loss negatively affected FD in proboscis length of pollinators, which was unaffected by relative exotic abundance (panels a+b). FD in proboscis diameter did not change along both gradients (c+d). FD in body length of pollinators decreased with natural habitat loss as well as increasing relative exotic abundance (e+f). Shown are effects of drivers from linear mixed-effects models (black line) and 95% confidence intervals (dashed lines). Effects are corrected for other covariates in models. Grey and black points show the underlying raw data for each pollinator assemblage on a given focal plant, with black points indicating significant deviation from null model distribution.

The additional statistical analyses supported previous results on changes in pollinator FD. Variation in plant species composition was not explained by increases in natural habitat loss across study sites (R^2 = 0.084, $F_{1,15}$ = 1.4, P = 0.12), and only few variation was related to relative exotic abundance (R^2 = 0.098, $F_{1,15}$ = 1.6, P = 0.029). Furthermore, including information on floral morphology of focal plants into statistical

models did not qualitatively or quantitatively alter previous results or substantially influence effect sizes of habitat loss and exotic plants (Table S3.3). Finally, including information on the phylogenetic structure of focal plant communities into our models led to a decrease in the effect of habitat loss on FD in proboscis length (Table S3.4). However, the overall negative effects of increasing natural habitat loss and relative exotic abundance on all other measures of functional diversity remained qualitatively and quantitatively similar (Table S3.4). In summary, effects of increasing natural habitat loss and relative exotic abundance were generally robust even when accounting for plant species-specific effects on pollinator FD. These results supported our conclusion that habitat loss and exotic plant invasion were the most important drivers of losses in FD.

We also quantified changes in weighted mean pollinator traits in order to assess the direction of changes in pollinator FD. Proboscis length of pollinators decreased with loss of natural habitat (Table 3.2; Fig. S3.2), while relative exotic abundance and the interaction of the two drivers only had a marginally negative effect (Table 3.2; Fig. S3.3). Multivariate analysis indicated that the decrease in proboscis length was mainly driven by a lower number of Lepidoptera (e.g. Lyceanidae, Pieridae) and a higher abundance of Diptera (e.g. Tephritidae, Calliphoridae) in sites with high habitat loss (Fig. S3.4). Proboscis diameter increased with loss of natural habitat (Table 3.2; Fig. S3.2), which again seemed to be driven by increases of particular Diptera families (e.g. Tephritidae, Sarcophagidae, Calliphoridae; Fig S3.4). Neither natural habitat loss nor relative exotic abundance had an effect on the mean body length of pollinators, indicating that the loss of FD in body length resulted from decreased variance in pollinator body length, or the loss of specifically-sized pollinators (Table 3.2; Figs S3.2+S3.4). Finally, mean body length of pollinators was larger on exotic than on native focal plants, but we found no differences with plant origin for the other functional traits (Table 3.2).

Table 3.2 Changes in weighted mean trait values of pollinator assemblages on native and exotic plants (131 focal plants) with natural habitat loss and increasing relative exotic abundance (17 plant–pollinator communities). Predictors were standardized to zero mean and unit variance.

	Proboscis length			Proboscis diameter			Body length		
Source of variation	**Estimate**	***Z***	***P***	**Estimate**	***Z***	***P***	**Estimate**	***Z***	***P***
Plant origin	0.25	1.6	0.12	-0.025	-0.68	0.49	1.8	2.2	0.029
Natural habitat loss	-0.24	-2.6	0.010	0.060	2.7	0.0064	-0.20	-0.41	0.68
Relative exotic abundance	-0.19	-1.7	0.092	0.0049	0.19	0.85	-0.14	-0.24	0.81
Natural habitat loss × Relative exotic abundance	-0.14	-1.7	0.085	-0.012	-0.61	0.54	0.048	0.11	0.91

Discussion

We found decreasing multivariate FD with increasing levels of natural habitat loss and relative exotic plant abundance. Importantly, responses of pollinator FD to the two global change drivers were trait-specific and thereby complementary. While natural habitat loss led to a decline of FD in proboscis length and body length, FD in body length also decreased with exotic plant abundance.

Multivariate FD of pollinators

Although pollinator FD is closely related to pollination processes and the stability of plant–pollinator communities (Fontaine et al. 2006; Albrecht et al. 2012) effects of ecosystem disturbance on pollinator FD are still poorly understood. Here we present the first study on the effects of multiple drivers of global change on pollinator FD, and demonstrate that both the loss of natural habitat and invasions by exotic plants have negative effects on multivariate pollinator FD. There are numerous studies that have

demonstrated a loss in species richness and abundance of pollinators in disturbed or invaded habitats (Kremen et al. 2002; Potts et al. 2010; Montero-Castaño and Vilà 2012 and references therein). Our study substantially contributes to these studies as we demonstrate that pollinator FD decreased independently from pollinator richness. Pollinator richness thus may be a poor representative of pollinator FD and consequently of ecosystem functioning (Díaz and Cabido 2001; Mayfield et al. 2010). Our findings also suggest that pollinator FD may already have declined in disturbed habitats in which pollinator richness is still unaffected. For example, the meta-analyses by Winfree et al. (2009) and Montero-Castaño and Vilà (2012) have shown that pollinator richness and abundance are almost unaffected by moderate habitat loss (e.g. 50% natural habitat cover remaining), and only significantly decrease when habitat loss is extreme (e.g. ≤ 5.0% natural habitat cover remaining). In our study, pollinator FD was already lower than expected at moderate levels of habitat loss (Figs 3.1+3.2), while pollinator richness was neither related to increasing natural habitat loss nor relative exotic abundance.

In addition to the negative effects of natural habitat loss, we detected a reduction of multivariate pollinator FD with increasing relative abundance of exotic plants. Exotic plants may especially favor generalized pollinators that are functionally similar, highly abundant and strong competitors (Johnson and Steiner 2000; Richardson et al. 2000b; Montero-Castaño and Vilà 2012). Low FD of pollinators in sites with high relative exotic abundance thus may be attributed to a loss in specialized pollinators with 'extreme' functional traits and a change towards pollinator assemblages with a more uniform trait composition. Particularly the dominance of a single or few exotic plant species in invaded habitats may severely diminish the diversity of floral resources and ultimately reduce native plant and related pollinator diversity (Cox and Elmqvist 2000; Traveset and Richardson 2006).

Importantly, although natural habitat loss and exotic plant abundance were comparable in generally reducing pollinator FD, the two drivers affected different pollinator traits. This illustrates the usefulness of separately investigating responses of individual pollinator traits to multiple drivers of global change (see also Williams et al. 2010). Different responses among pollinator traits to natural habitat loss and exotic plant abundance may also explain the absence of interactive (e.g. synergistic) effects of the two global change drivers on univariate and multivariate FD. In the following, we disentangle

the detected changes in multivariate FD of pollinators by separately investigating changes in FD of individual traits.

Trait-specific changes in FD of pollinators

Loss of natural habitat led to a reduction of FD in proboscis length of pollinators. Investigating changes in mean proboscis length suggested that this reduction was mainly caused by a loss in long-tongued butterflies. Accordingly, multivariate analysis showed that butterfly families were generally absent from study sites with high degree of habitat loss. Loss of natural habitat may negatively affect butterflies via a loss in habitat connectivity and a reduced abundance of suitable host plants (Woodhall 2005; Brückmann et al. 2010). Increasing relative exotic abundance reduced the average proboscis length of pollinators as well, although the effect was only marginal. Possibly, exotic plants attracted abundant generalist pollinators with short to medium-sized proboscides (e.g. the native pollinator *Apis mellifera*). However, long-tongued pollinators are often important agents in specialized pollination systems (e.g. Johnson and Steiner 2000; Pauw et al. 2009). Reduced abundance of these long-tongued pollinators in disturbed habitats may particularly negatively affect the pollination of plant species with deep nectar holders (Pauw et al. 2009; Stang et al. 2009).

Similarly to the changes in proboscis length, we recorded shifts in the composition of proboscis diameters with natural habitat loss. Pollinators with the widest proboscides were mostly flies, e.g. species of the genera *Didacus* (Tephritidae) and *Psilodera* (Acroceridae), which may prevail in disturbed habitats. Accordingly, Calliphoridae and Sarcophagidae were most abundant in study sites with low remaining natural habitat cover. The increase in the mean diameters of proboscides may prevent efficient pollination when nectar holders are very narrow. Thus, while some nectar resources may already be inaccessible to short-tongued pollinators of Diptera families, their comparably wide proboscides may impose an additional constraint. Particularly plant species with an otherwise generalized pollination syndrome (e.g. plants of the Asteraceae family) often have a narrow nectar holder (Stang et al. 2009).

Functional diversity in body length decreased with natural habitat loss, yet mean body length was unaffected. Thus, habitat loss seemed to decrease the variance in differently sized pollinators, and especially seemed to negatively affect small (Greenleaf et

al. 2007) and comparably large (e.g. butterflies; Brückmann et al. 2010) pollinators. Moreover, complementing the effects of natural habitat loss, FD in the body length of pollinators decreased with increasing relative exotic abundance. As the diversity of plant resources and of pollinators are strongly linked to one another (Potts et al. 2003), particularly the dominance of floral resources by a single or few highly abundant exotic plant species (e.g. *L. camara* or *A. mearnsii*) may have reduced the FD in body length (Traveset and Richardson 2006; Potts et al. 2010). For example, invaded study sites in which the butterfly-pollinated *L. camara* was most abundant supported relatively high abundances of butterflies (given that natural habitat cover was sufficient, personal observation). Contrastingly, study sites with high abundance of *A. mearnsii* were mainly dominated by Hymenoptera (e.g. the native honeybee *Apis mellifera*). Consequently, plant–pollinator communities with high relative abundance of single or few exotic plant species may lack those small or large pollinators that by their functional complementary promote pollination of the remaining native plant species (Blüthgen and Klein 2011; Albrecht et al. 2012).

Consequences for pollination effectiveness

In this study we treated all flower visitors as potential pollinators. However, visitors differ greatly in their pollination effectiveness, and even diverse visitor assemblages may include only few legitimate pollinators (Herrera 1987; King et al. 2013). Visitor identity thus is often more important for pollination success than for instance visit duration or frequency (King et al. 2013; but see Vázquez et al. 2012). For example, floral visitors with short proboscides often act as pollen thieves when plants have deep nectar holders (e.g. Hargreaves et al. 2012). Plants adapted to long-tongued pollinators in turn may show reduced levels of cross-fertilization, with consequences for the ratio of different flower morphs in a population (Simón-Porcar et al. 2013) or co-evolutionary processes (Pauw et al. 2009). Loss of pollinator FD in proboscis length and of long-tongued pollinators in disturbed habitats may therefore severely negatively affect pollination of specialized plant species. Yet, floral traits often fail in predicting effective pollinators and vulnerability of specialist plants to habitat disturbance (Aizen et al. 2002). Species of the genus *Asclepias* for instance are generally believed to be butterfly-pollinated, yet bees are often more effective (Fishbein and Venable 1996). Similarly, although a small body size may reduce

the amount of transported pollen, high visitation rates of small to medium-sized Hymenoptera may outweigh visits of larger but also rarer visitors (Herrera 1987; Fishbein and Venable 1996). In other words, a pollinator species seldom is highly abundant and at the same time an efficient visitor (Herrera 1989). In summary, high pollinator FD may be especially relevant for the stability and persistence of diverse plant–pollinator communities (Fontaine et al. 2006), yet we predict the effects of FD of pollinator assemblages on most plant species to vary plant-specifically.

Conclusions

Here we show a reduction in the FD of pollinators with increasing magnitude of two major drivers of global change, i.e. loss of natural habitat and exotic plant invasion. Our results show that these drivers have complementary negative effects when they affect different functional traits of pollinators. This result would have been overlooked in a single-driver study or a study focusing solely on pollinator richness. Furthermore, we found that decreases in the FD of pollinators went beyond those in pollinator richness and that pollinator richness was not related to either of the two drivers. Pollinator richness thus is a poor representative of pollinator FD and likely of pollination processes. We suggest that investigating patterns in pollinator FD along environmental gradients substantially improves understanding and predictions of effects of global change on pollination processes, especially when multiple pollinator traits and drivers of global change are considered.

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4 Guild-specific shifts in visitation rates of frugivores with habitat loss and plant invasion

With Dana G. Berens & Nina Farwig

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Abstract

Habitat loss and plant invasions are two major drivers of global change in subtropical and tropical ecosystems. Both lead to a loss of biodiversity and alter species interactions, which may imperil vital ecosystem processes such as seed dispersal by frugivores. Reponses of frugivores to disturbance are often linked to their specialization on certain habitats or resources. Yet, it is poorly understood how habitat loss and plant invasion structure interactions between plants and different habitat or feeding guilds. Here we investigated whether visitation rates of frugivores change guild-specifically with increasing habitat loss and invasion level in a heterogeneous subtropical landscape. In 756 h of observations, we recorded 1446 plant–frugivore interactions among 18 plant species and 42 avian frugivore species. Visitation rates of forest specialists decreased with increasing habitat loss, but not with changes in invasion level. In contrast forest generalists and forest visitors were unaffected by either driver. Similarly, obligate frugivores that overall showed a generalized fruit choice were unaffected by habitat loss and changes in invasion level. Contrary, visitation rates of specialized partial and opportunistic frugivores decreased with higher invasion level. Importantly, the negative effect of plant invasion on partial frugivores was more pronounced as habitat loss in the same study site increased, indicating a synergistic effect of the two drivers. The implications of our study are twofold: first, frugivores respond guild-specifically to habitat loss and plant invasion. Thereby forest dependency is mainly related to habitat loss, and degree of frugivory mainly related to plant invasion. Forest generalists and obligate frugivores in turn may play a key-role for forest regeneration in disturbed forest landscapes. Second, particularly frugivores with a specialized fruit choice may be threatened by synergistic effects between habitat loss and plant invasion.

Introduction

The ongoing loss of natural habitats and changes in the composition of species communities through biotic invasions are two of the most prominent drivers of global change (Vitousek et al. 1997; Sala et al. 2000). These two drivers alter patterns in biodiversity and affect ecosystem processes, which are vital to the persistence and stability of species communities (Tylianakis et al. 2008). In subtropical and tropical forests, seed dispersal by frugivorous animals is an important ecosystem process in the regeneration of the great majority of woody plant taxa (Jordano 2000; Sekercioglu 2006). Both natural habitat loss and plant invasions have the potential to fundamentally alter plant–frugivore communities and seed dispersal processes (Farwig and Berens 2012; McConkey et al. 2012).

Changes in community composition with disturbance are usually linked to the functional traits of the species that form these communities (McGill et al. 2006). Important functional traits that structure frugivore communities are differences in dependencies of frugivores on forest habitat and fruiting plant resources (Newbold et al. 2013). Frugivores thus are often classified into functional guilds according to their forest dependency and degree of frugivory (e.g. Dennis and Westcott 2006; Farwig et al. 2006). In turn, responses of frugivores to habitat loss or plant invasion have been shown to be guild-specific (e.g. (e.g. Tscharntke et al. 2008). Forest loss generally affects forest specialists more negatively than forest generalists or forest visitors (e.g. Neuschulz et al. 2011; Newbold et al. 2013). Whether plant invasion induces similar negative effects on forest specialists depends on the potential of the invader to render habitat conditions unsuitable for specialists. Invasive trees such as *Psidiuam guajava* that become part of the natural forest community can attract forest specialists, generalists and visitors alike (Berens et al. 2008). In contrast, a high abundance of shrubby invasive plants such as *Lantana camara* can selectively favor frugivores adapted to lower vegetation, whereas forest specialists of the canopy decline (Aravind et al. 2010). Moreover, both habitat loss and plant invasion often induce changes in fruiting resource abundance and composition. The responses of frugivores to these changes are thereby related to their degree of frugivory. Overall, the abundance of fruiting resources in subtropical and tropical ecosystems shows strong temporal and spatial fluctuations (e.g. Mulwa et al. 2013). Obligate frugivores which are highly dependent on fruiting resources thus should have a more generalized foraging

behavior than partial or opportunistic frugivores, which may feed more specifically on preferred fruit resources (MacArthur and Pianka 1966; Schleuning et al. 2012). Given that sufficient fruit resources remain, obligate frugivores may prevail in forest landscapes, which are heavily degraded by habitat loss or plant invasion. In contrast, comparably more specialized partial and opportunistic frugivores may be prone to disappear from plant–frugivore networks with changes in habitat or resource conditions. As invasive fruits often become an important part in the diet of unspecialized frugivores (Deckers et al. 2008; McConkey et al. 2012), obligate frugivores may further play a key role for seed dispersal of native and invasive plants in degraded forests.

Most studies so far have focused on single model organisms to assess shifts in the relative importance of specific frugivore guilds for seed dispersal with forest disturbance (e.g. Berens et al. 2008; Lehouck et al. 2009; Neuschulz et al. 2011). Results of these studies vary among the focal species, and may not be representative for effects occurring on the scale of communities (Farwig and Berens 2012). Consequently, understanding effects of forest disturbance on plant–frugivore interactions considerably benefits from a community-level approach (Farwig and Berens 2012). However, quantitative analyses on the level of whole plant–frugivore communities are still rare, and mostly focus on modification or loss of natural habitat, whereas plant invasions have received far less attention (e.g. Albrecht et al. 2013; Chama et al. 2013; but see e.g. Heleno et al. 2013). Further, it remains generally unknown whether multiple drivers of global change, e.g. habitat loss and plant invasion, do also exceed interactive, e.g. synergistic, effects on plant–frugivore interactions (Didham et al. 2007). Such interactive effects could particularly threaten specialized plant–frugivore interactions (Tylianakis et al. 2008; McConkey et al. 2012).

Here we present a community approach on guild-specific changes in plant–frugivore interactions with different degrees of habitat loss and plant invasion in a heterogeneous subtropical landscape. We used visitation rates as an estimate of the relative importance of different frugivore guilds for seed dispersal of a given plant species (Vázquez et al. 2005). Overall, we expected a decrease in frugivore visitation rates following habitat loss and plant invasion, respectively. Yet, within plant–frugivore communities, we expected responses of frugivores to be guild-specific. More specifically, we expected generalized frugivores such as forest generalists and obligate frugivores to be unaffected by habitat

loss and plant invasion. In contrast, we expected a decline of specialized frugivores, e.g. forest specialists, partial and opportunistic frugivores, with both drivers. Thereby, we expected negative synergistic effects of habitat loss and plant invasion on visitation rates of comparably specialized frugivores. Finally, we hypothesized that generalized species, i.e. forest generalists and obligate frugivores, are the most important frugivores feeding on invasive plant species.

Methods

Study region

We conducted our study in a heterogeneous subtropical landscape within and around Oribi Gorge Nature Reserve (30°41'S, 30°17'E, 1,850 ha), situated near the South coast of South Africa's KwaZulu-Natal province. Annual temperatures in this area range from 8 to 28°C and rainfall ranges from 660 to 1200 mm (von Maltitz 2003). The region's natural vegetation is mainly characterized by patches of indigenous scarp forest, which are interspersed by natural grassland. Scarp forests are of conservation priority due to their high biodiversity, degree of endemism and high importance for forest dependent species (Eeley et al. 2001). However, these forests have been dramatically reduced in their distribution and extent as a consequence of intensive agriculture and urban sprawl (von Maltitz 2003). Additionally, as in most other parts of South Africa, fleshy-fruited invasive plants such as *L. camara* (Verbenaceae), *Solanum mauritianum* (Solanaceae) or *Cinnamonum camphora* (Lauraceae) have become highly abundant in the region, and frequently dominate the fruiting plant community at scarp forest edges. Consequently, large undisturbed scarp forests are generally confined to protected areas, and only few mostly small and invaded forest remnants remain within the sugarcane-dominated agricultural matrix.

Study design

In January 2012, we selected nine study sites, located in forests within and around Oribi Gorge Nature Reserve. Mean pair-wise distance between study sites was 4.9 ± 0.4 km (mean ± standard error [SE] throughout). We located all study sites at forest edges or gaps to take into account edge effects potentially present in forest fragments but not in continuous forests. Further, study sites varied along two independent environmental

predictor variables, each representing one global change driver: habitat loss and level of plant invasion ('low' or 'high'). For habitat loss, we quantified the proportion of natural habitat cover in a 1500 m radius around the center of study sites using ArcInfo GIS 9.3 and a freely available land cover data set (satellite imagery from 2008, 20 m resolution; unpublished GIS data provided by Ezemvelo KZN Wildlife). Natural habitats included natural forest as well as natural woodland and bushland. As described above, also natural grasslands occur in the region, yet these comprised only a negligible proportion of the total natural habitat cover across study sites and rarely harbored fruiting plant species. Natural grassland was therefore not included in our estimation of natural habitat cover. We defined habitat loss as the proportion of all other, non-natural, habitats on the total area covered by our 1500 m radii ('habitat loss' hereafter). Habitat loss ranged from 0.33 to 0.93 (0.71 ± 0.071) across study sites. To estimate the level of plant invasion, we a priori chose study sites, which showed low or high proportions of invasive plant species. We then established permanent transects of 250 m length × 20 m width along forest edges of study sites. Every 10–14 days, we conducted transect walks, identified all fleshy-fruited plant species and estimated their fruit abundance. We identified fruiting plant species and their origin (native or invasive) following Boon (2010). We calculated the mean proportion of the invasive fruit abundance on the total fruit abundance for a given study site over all transect walks. These proportions showed a strong bimodal distribution: four study sites featured low proportions of invasive fruits (0.00–0.24; mean ± SE = 0.076 ± 0.056), five study sites high proportions (0.79–0.96; 0.88 ± 0.031). Accordingly, we categorized the level of plant invasion of our study sites into 'low' and 'high', respectively ('invasion level' hereafter). Study sites were chosen in a way that habitat loss and invasion level were not related to one another (ANOVA: $F_{1,7} = 1.2$, $P = 0.32$). Further, neither habitat loss (Pearson correlation: $r = -0.11$, $n = 9$, $P = 0.78$) nor invasion level ($F_{1,7} = 0.41$, $P = 0.55$) was related to the mean fruit abundance per study site.

Survey of plant–frugivore interactions

We conducted observations of plant–frugivore interactions from February to April 2012. We observed all fleshy-fruited plant species bearing at least 50 ripe fruits in a radius of 150 m around the center of study sites. Observed plant species richness ranged from 3 to 6 (4.7 ± 0.41) across study sites. Observations were conducted for six hours from sunset and

only took place in suitable weather conditions, i.e. no heavy rain or high wind velocity. We observed each focal plant species for three times, and chose different fruiting individuals where possible ($18\ h \times plant\ species^{-1} \times study\ site^{-1}$). Observations were conducted randomly among sites and species. Birds constituted the majority of the observed plant–frugivore interactions (1446 of 1468 plant–frugivore interactions in total; 99%). Additionally, we recorded 22 plant–frugivore interactions by two monkey species (Vervet monkey [*Cercopithecus aethiops*]: 9 interactions; Samango monkey [*Cercopithecus mitis*]: 13 interactions). Although we conducted all frugivore observations from a camouflaged hide, monkey species were frequently disturbed by our presence. As observations of feeding monkeys thus were not standardized, we omitted the two monkey species from all following analysis. Birds were identified according to Chittenden (2007).

To assess guild-specific changes in visitation rates of frugivores with changes in habitat conditions, we divided frugivores into functional guilds (Table S4.2 in the Appendix). We therefore assessed the forest dependency (forest specialist, forest generalist, forest visitor) and the degree of frugivory (obligate, partial, opportunistic) of each frugivore species. For forest dependency, we followed the criteria outlaid in Farwig et al. (2006), using species-specific information given in Hockey et al. (2005). Generally, forest specialists only occur and breed within undisturbed forest, whereas generalists also can occur and breed in disturbed forests. Forest visitors are overall more common in non-forest habitats (Farwig et al. 2006). Degree of frugivory was obtained from Kissling et al. (2007). If a species was not listed in Kissling et al. (2007) we obtained the degree of frugivory from Hockey et al. (2005). Generally, the primary food items of obligate frugivores are fruits, whereas major food items of partial frugivores also encompass non-fruit resources, e.g. invertebrates. Opportunistic frugivores only occasionally feed on fruits to supplement their diet (Kissling et al. 2007).

Statistical analysis

For each study site, we compiled a quantitative plant–frugivore interaction matrix based on the interaction frequencies of observed frugivore species and plant species. We defined interaction frequencies as the number of fruit consuming individuals of a frugivore species on a given plant species. We only included individuals that were potential seed dispersers,

i.e. either swallowed fruits (72% of interactions), pecked on fruits (27%), or carried fruits in their beak away from the mother plant (1.8%).

We then used visitation rates as an estimate of the relative importance of different frugivore guilds for seed dispersal of a given plant species (Vázquez et al. 2005). We conducted two separate analyses, the first focusing on guild-specific changes in visitation rate as a consequence of differences in forest dependency of frugivores, the second on changes as a consequence of differences in degree of frugivory. For each analysis, we aggregated visitation rates of frugivores as the summed visits of frugivore species within a given guild (e.g. for forest dependency we summed the visitation rates of forest specialists, forest generalists and forest visitors, respectively, on a given plant species).

As we were investigating visitation rates of different frugivore guilds on plant species within study sites, our statistical analyses must account for the hierarchical design of our study. We therefore fitted generalized linear mixed-effects models with Poisson error distribution, and included frugivore guild, plant species and study site as random effects. Most of the investigated plant species in this study were present in multiple study sites, yet no plant species was present in all sites. We thus fitted plant species and study site as separate random factors, corresponding to a partially crossed design. In contrast, we fitted frugivore guild as a nested factor within plant species, according to a fully crossed design with information on visitation rates for every guild on a given plant species. Plant origin (native vs. invasive), habitat loss and invasion level per study site were fitted as predictors. To assess the within study site preferences of specific frugivore guilds between native and invasive plant species, we fitted the two-way interaction of frugivore guild and plant origin. To assess additive and potential interactive effects of habitat loss and invasion level on guild-specific visitation rates across sites, we fitted the three-way interaction between frugivore guild, habitat loss and invasion level. Finally, to account for differences in fruit abundance of plant species, we included the mean fruit abundance (ln-transformed) of each plant species recorded during the three observation session as covariate. The statistical notation of the global models thus read as

1) visitation rate ~ ln(fruit abundance) + frugivore guild × (plant origin + habitat loss × invasion level) + (1 | plant species / frugivore guild) + (1 | study site)

with frugivore guild reflecting the guilds within forest dependency and degree of frugivory, respectively.

We then simplified each global model to retain a minimum adequate model that included only the most likely combination of predictors. Based on the two global models, we generated two model sets; one for guild-specific changes in visitation rates with forest dependency and degree of frugivory, respectively. Each model set included all possible submodels of the respective global model and one model including only the intercept (104 models in a given model set; Tables S4.3+S4.4). We then inferred the likelihood of every model within a given model set using Akaike's information criterion for small sample sizes (AIC_c). The model with the lowest AIC_c was chosen as the 'best' or minimum adequate model that predicted frugivore visitation rate (Bolker et al. 2009). Further, we calculated Akaike weights for every model and estimated the relative importance of a predictor across a given model set as the summed Akaike weights of each model in which the respective predictor appeared. Thus, Akaike weights of predictors give information on the relative importance of a predictor in contributing to the most likely models in a model set. Akaike weights range from 0 to 1, with higher values indicating higher relative importance.

To verify our assumption that obligate frugivores had a more generalized foraging behavior than partial or opportunistic frugivores, we analyzed whether the number of plant partners (i.e. species degree; ln-transformed) differed with degree of frugivory. Obligate frugivores on average visited more different plant species (backtransformed mean ± SE: 5.6 + 2.5, -1.7) than partial (2.6 + 0.70, -0.55) or opportunistic frugivores (1.3 + 0.16, -0.14; ANOVA: $F_{2,39} = 11$, $P < 0.0010$).

For each minimum adequate model, we tested for spatial correlation in the residuals (Moran's *I*) in discrete distance classes of 4000 m. No spatial correlation was detected in any distance class (Moran's *I* close to zero and $P \geq 0.14$ in all cases). We fitted all generalized linear mixed-effects models using a Laplace likelihood approximation (Bolker et al. 2009). Residuals of minimum adequate models were normally distributed and showed no clear trends in relation to fitted values, indicating that models were statistically robust. To facilitate comparison of effect sizes, we *z*-transformed all continuous predictors (standardized to zero mean and unit variance). All statistical analyses were conducted in R 2.15.2 (R Development Core Team 2012) with add-on packages 'lme4' (Bates et al. 2012)

for generalized linear mixed-effects models, 'MuMIn' (Barton 2013) for generation of model sets, and 'ade4' (Dray and Dufour 2007) for testing spatial correlation.

Results

In 756 h of observations, we recorded 1446 plant–frugivore interactions among 18 different plant species and 42 avian frugivore species (Tables S4.1+S4.2). Several of these plant species were present in multiple study sites, and we thus conducted a total of 42 plant observations (each 18 h) during the study period.

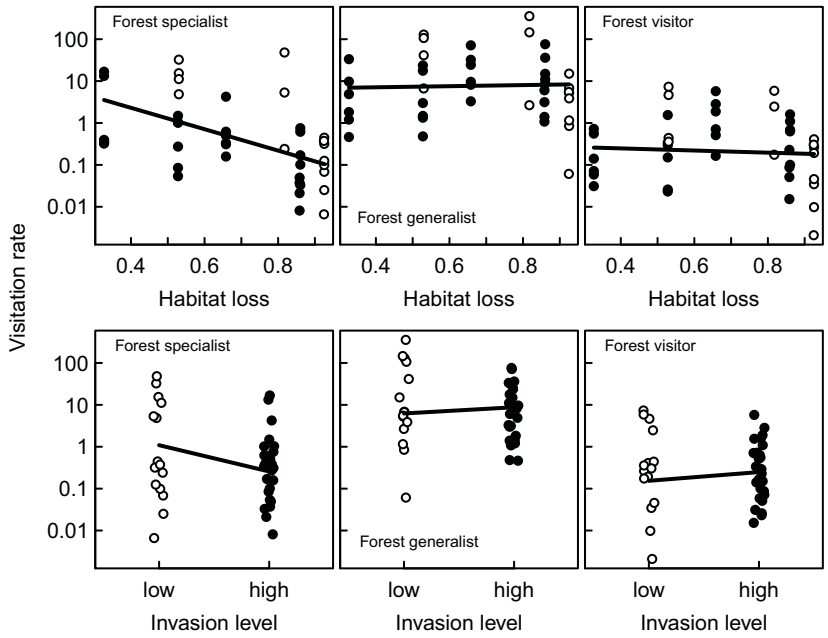

Fig. 4.1 Changes in frugivore visitation rates of different habitat guilds with natural habitat loss and level of plant invasion in a subtropical forest landscape. Shown are effect sizes (lines) and fitted data (circles) of the minimum adequate generalized linear mixed-effects model. Open circles refer to plants in study sites with low invasion level, filled circles to plants in sites with high invasion level. For the effect of invasion level, fitted values are slightly jittered for better visualization. Note the logarithmic scale for visitation rate.

Based on differences in forest dependency, visitation rates within 18 h of observations were lower for forest specialists (3.9 ± 1.5) than for forest generalists (30 ± 9.7), but higher than for forest visitors (1.1 ± 0.40; Table 4.1). Overall, visitation rates increased with higher fruit abundance of a given plant species (Table 4.1). As expected, visitation rates of forest specialists decreased with increasing habitat loss. In contrast, despite a slight decrease, this effect was not significant for a higher invasion level (Table

4.1, Fig. 4.1). Compared to forest specialists, forest generalists and forest visitors were neither affected by increasing habitat loss nor by changes in invasion level across study sites (Table 4.1, Fig. 4.1). Plant origin or its interaction with frugivore guild was not included in the minimum adequate model, indicating low importance of plant origin for overall visitation rates and within study site differentiation of frugivore guilds. Further, habitat loss and invasion level did not exert an interactive effect on visitation rates of frugivores grouped by their forest dependency.

Table 4.1 Minimum adequate model of changes in frugivore visitation rates of different habitat guilds (forest specialist, forest generalist, forest visitor) with increasing habitat loss and invasion level in a subtropical forest landscape. Akaike weights give information on the relative importance of predictors across all possible models in the model set. Also shown are predictors which were not included in the final model, sorted by decreasing relative importance. Note that forest specialists form the intercept.

Source of variation	Estimate	SE	*Z*	*P*	Akaike weight
Fruit abundance	1.3	0.12	11	< 0.001	1.0
Forest dependency					1.0
Forest generalists	1.9	0.41	4.2	< 0.001	
Forest visitors	-2.0	0.51	-3.8	< 0.001	
Habitat loss	-1.2	0.52	-2.3	0.020	1.0
Invasion	-1.4	0.95	-1.5	0.13	1.0
Forest dependency x Habitat loss					1.0
Forest generalists x Habitat loss	1.3	0.28	4.6	< 0.001	
Forest visitors x Habitat loss	1.1	0.40	2.8	0.0060	
Forest dependency x Invasion					1.0
Forest generalists x Invasion	1.8	0.37	4.8	< 0.001	
Forest visitors x Invasion	1.9	0.50	3.8	< 0.001	
Not included					
Plant origin					0.52
Habitat loss x Invasion					0.29
Forest dependency x Plant origin					0.13
Forest dependency x Habitat loss x Invasion					0.042

Based on differences in degree of frugivory, obligate (15 ± 4.0) and partial frugivores (17 ± 8.8) showed similar visitation rates, but opportunistic frugivores (2.7 ± 1.5) were only rarely observed (Table 4.2). Again, total visitation rates increased with fruit abundance (Table 4.2). While visitation rates of obligate frugivores were not significantly affected by increasing habitat loss or invasion level, visitation rates of partial frugivores decreased in study sites with high invasion level (Table 4.2, Fig. 4.2). Moreover, the decrease in visitation rates of partial frugivores in invaded study sites became even more pronounced as habitat loss increased, indicating a negative synergistic effect of the two global change drivers (Table 4.2, Fig. 4.2). Visitation rates of opportunistic frugivores were unaffected by habitat loss, yet lower in study sites with high than with low invasion level (Table 4.2, Fig. 4.2). Similar to forest dependency, plant origin and its interaction with frugivore guild was not included in the minimum adequate model.

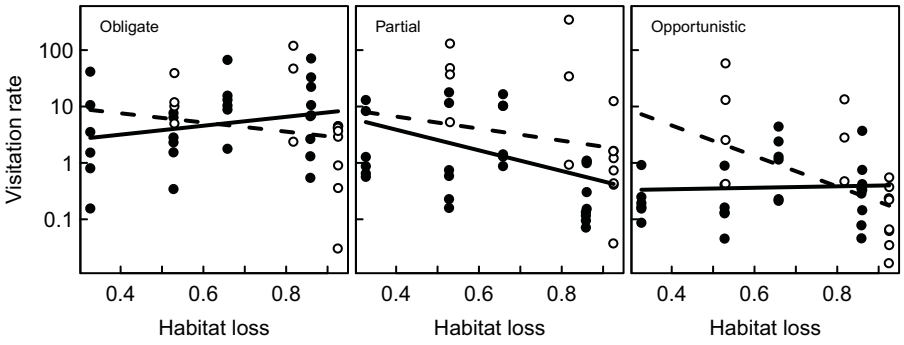

Fig. 4.2 Interactive effects of natural habitat loss and invasion level on frugivore visitation rates of different feeding guilds in a subtropical forest landscape. Shown are effect sizes (lines) and fitted data (circles) of the minimum adequate model. Dashed lines and open circles represent the guild-specific effects of habitat loss in study sites with low invasion level, solid lines and closed circles in sites with high invasion level. Note the logarithmic scale for visitation rate.

Table 4.2 Minimum adequate model of changes in frugivore visitation rates of different feeding guilds (obligate, partial, opportunistic) with increasing habitat loss and invasion level in a subtropical forest landscape. Akaike weights give information on the relative importance of predictors across all possible models in the model set. Also shown are predictors which were not included in the final model, sorted by decreasing relative importance. Note that obligate frugivores form the intercept.

Source of variation	Estimate	SE	*Z*	*P*	Akaike weight
Fruit abundance	1.2	0.11	10	< 0.001	1.0
Degree of frugivory					1.0
Partial	-0.30	0.44	-0.68	0.50	
Opportunistic	-1.7	0.52	-3.3	< 0.001	
Habitat loss	-0.39	0.74	-0.53	0.60	1.0
Invasion	0.18	0.86	0.21	0.83	1.0
Habitat loss x Invasion	0.77	0.90	0.85	0.39	0.96
Degree of frugivory x Habitat loss					1.0
Partial x Habitat loss	-0.12	0.28	-0.44	0.66	
Opportunistic x Habitat loss	-0.91	0.49	-1.9	0.065	
Degree of frugivory x Invasion					1.0
Partial x Invasion	-1.2	0.24	-5.0	< 0.001	
Opportunistic x Invasion	-0.92	0.45	-2.1	0.038	
Degree of frugivory x Habitat loss x Invasion					0.95
Partial x Habitat loss x Invasion	-1.1	0.34	-3.3	< 0.001	
Opportunistic x Habitat loss x Invasion	0.59	0.61	0.98	0.33	
Not included					
Plant origin					0.34
Degree of frugivory x Plant origin					0.021

Discussion

Here we show guild-specific changes in visitation rates of frugivores with habitat loss and plant invasion. While forest generalists and obligate frugivores were overall unaffected by increasing habitat loss or a high level of plant invasion across study sites, visitation rates of comparably more specialized frugivores decreased. More specifically, visitation rates of forest specialists decreased with increasing habitat loss, and visitation rates of partial and

opportunistic frugivores decreased with high invasion level. Importantly, the negative effect of plant invasion on partial frugivores was even more pronounced in study sites with high habitat loss, indicating a synergistic effect of habitat loss and plant invasion on specialized plant–frugivore interactions.

Recent studies have shown that interactions between fleshy-fruited plant species and their seed dispersers are highly context-dependent (e.g. Perea et al. 2013). Accordingly, the observed frugivores in this study showed guild-specific responses to increasing habitat loss and differences in invasion level across study sites. Thereby, frugivore responses were related to their forest dependency and degree of frugivory. While visitation rates of forest specialists decreased, visitation rates of forest generalists and forest visitors were overall unaffected by increasing habitat loss, i.e. forest cover in the surrounding landscape. Thus, forest generalists or forest visitors seem to be able to persist even when only little forest cover remains in the landscape matrix. In contrast, forest specialists are usually the first frugivores to disappear in disturbed forest landscapes (e.g. Tscharntke et al. 2008; Neuschulz et al. 2011). Large, non-migratory frugivores are particularly vulnerable, as they are usually unable to compensate the loss of natural habitats in agriculturally used forest landscapes (Newbold et al. 2013). Here, we limited our sampling of plant–frugivore interactions to forest edges, and it should be noted that therefore we may have underestimated the abundance of specialist frugivores of the forest interior. This may explain the overall low visitation rates of forest specialists as compared to forest generalists. However, our results can also be seen as a conservative estimate of the negative effect of habitat loss on specialists, as their decline may be even more pronounced when comparing the interior of large connected forests to edges of forest remnants

In contrast to habitat loss, frugivore responses to changes in invasion level were not related to their degree of forest dependency, despite a slight yet not significant decrease of forest specialists in study sites with high invasion level. This contrasts with studies showing that invasive plants may alter habitat conditions (e.g. forest cover), which can result in a reduced abundance of forest specialists of the canopy (e.g. Aravind et al. 2010). Invaded forests in our study region still seem to sustain habitat conditions, which are suitable for forest specialists (e.g. high fruiting plant richness and dense canopy covers; Chama et al. 2013). An explanation is that invasive plants mainly dominated at forest

edges, whereas the forest interior often still showed near-natural conditions. Again, as we limited our sampling to forest edges the result that forest specialists prevailed in invaded study sites should therefore be considered a conservative estimate.

As expected, we further found shifts in visitation rates of frugivores dependent on their degree of frugivory. Here, similar to the high robustness of forest generalists and forest visitors to habitat loss and plant invasion, visitation rates of obligate frugivores were overall unaffected by habitat loss and invasion level. Thus, obligate frugivores may disproportionally contribute to seed dispersal processes in degraded forest landscapes, which is likely the result of their high flexibility in fruit choice with changes in resource abundance and diversity (Schleuning et al. 2012; Mulwa et al. 2013). This flexibility is further often the key to the integration of invasive plants into native food webs (Traveset and Richardson 2006). In contrast, visitation rates of the comparably more specialized partial and opportunistic frugivores decreased in study sites with high invasion level. Interestingly, this reduction affected native and invasive plants alike, as we found no effect of plant origin on visitation rates of different frugivore guilds, and further no changes in this pattern with differences in invasion level (interaction among frugivore guild × plant origin × invasion level not significant; data not shown). Plant invasion in our study thus seemed to have altered habitat and resource conditions in such a way that a large fraction of partial and opportunistic frugivores only rarely visited highly invaded study sites. Habitat alterations may include a decrease in habitat quality via shrub encroachment of the main invader *L. camara* (Aravind et al. 2010) and changes in nutrient composition due to differences in fruit traits between native and invasive plant species (Gosper and Vivian-Smith 2009). These more subtle differences in species-specific preferences of frugivores could not be covered by our classification into different frugivore guilds and require further investigation. Still, our results strongly suggest that ongoing eradication of invasive plants in the study area is crucial for forest conservation in the long term. Strikingly, for partial frugivores the negative effect of plant invasion was even more pronounced in study sites with lower remaining forest cover in the surrounding landscape matrix. This corroborates that habitat loss and exotic plant invasions may interactively structure species interactions, with negative effects for specialized species (Didham et al. 2007; Tylianakis et al. 2008). Interactive effects of different global change

drivers on plant–frugivore interactions have rarely been studied and should receive more attention (McConkey et al. 2012).

The observed shifts in guild composition towards a prevalence of habitat generalists and obligate frugivores in disturbed forests landscapes may have important consequences for patterns in seed dispersal and consequently forest regeneration. Unspecialized frugivores such as forest generalists or obligate frugivores often form part of the central core of plant–frugivore networks, and retain the reliability of seed dispersal processes in disturbed forest landscapes (e.g. Albrecht et al. 2013). However, the loss of forest specialists can translate into changes in seed dispersal if frugivores are nonredundant in their roles as dispersal vectors (Jordano et al. 2007; McConkey and Brockelman 2011). For example, seed dispersal of large-fruited plants can be significantly reduced if large-bodied dispersers disappear from small forest fragments (Wotton and Kelly 2011). Guild-specific changes of frugivores with habitat loss and plant invasion as observed in this study thus may have direct consequences for seedling distribution and the genetic structure of plant populations (Voigt et al. 2009). Overall, understanding differences in the functional complementarity and seed dispersal effectiveness of different frugivores remains an important challenge (Schupp et al. 2010). As shown here, effects of habitat loss and plant invasion on frugivory may vary between different functional traits (i.e. forest dependency or degree of frugivory), which highlights the need to investigate multiple response traits on a community scale. Further, synergistic effects of habitat loss and plant invasion can play an important role in interaction shifts (Didham et al. 2007; Tylianakis et al. 2008). Such shifts may especially imperil specialized interactions, which may eventually result in native species decline. Finally, combining plant–frugivore observations with on-the-ground assessments of seedling and adult tree distributions and their genetic makeup could reveal whether shifts in frugivore communities translate into changes in forest regeneration patterns.

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5 Synthesis

Natural habitat loss and exotic plant invasions are two major drivers of global change in subtropical and tropical ecosystems. These two drivers lead to a loss of biodiversity and alter species interactions, which may imperil vital ecosystem functions and services such as pollination and seed dispersal by animals. Yet, additive and potential interactive effects of natural habitat loss and plant invasion on mutualistic interactions are poorly understood. I therefore studied the combined effects of these two drivers on plant–pollinator and plant–frugivore interactions in a heterogeneous forest landscape in South Africa.

First, across 17 study sites that differed in the magnitude of the effects of the two global change drivers, I investigated interaction networks of plants and their pollinators. I aimed at understanding whether the two drivers led to a loss of specialized plant–pollinator interactions, and used multivariate analyses in order to investigate whether this loss was accompanied by a species-turnover towards generalist pollinators with habitat loss and relative abundance of exotic plants. I found that visitation rates of pollinators to native plants increased with both increasing natural habitat loss and relative exotic abundance, respectively. On the contrary, exotic plants seemed only weakly integrated into plant–pollinator interaction networks. Specialization of plants on pollinators and vice versa decreased along both gradients. Decreasing pollinator specialization thereby seemed to be driven by changes in the composition of pollinator communities towards habitat generalists in study sites affected by natural habitat loss or exotic plant invasion. In all cases, effects of the two global change drivers were solely additive. In summary, natural habitat loss and exotic plant invasion seemed to promote generalist plants and pollinators, and likely led to the loss of specialized plant–pollinator interactions. Pollinators generally seemed to prefer native plants to exotic plants, which may have been driven by constraints imposed by functional traits of exotics, differences in the availability of floral resources between native and exotic plants, and lag-times in the establishment of interactions between exotic plants and native pollinators. The additive effects of the two drivers on pollinator visitation and specialization of plant–pollinator interactions would have been overlooked in a single-factor study.

Second, I used the trapped pollinators of the first study presented in this thesis to investigate whether the functional diversity (FD) of pollinator assemblages on plant species was reduced in sites with low natural habitat cover or high relative abundance of exotic plants. I investigated univariate and multivariate FD of pollinators in three functional traits that are closely linked to pollination processes: proboscis length,

proboscis diameter and body length. Here, I focused on understanding whether the two global change drivers had an overall negative effect on pollinator FD, but also whether effects of the two drivers differed between functional traits, and whether effects were additive or interactive. I found that the FD of pollinators decreased with natural habitat loss and increasing relative exotic plant abundance per study site, respectively. The negative effects of the two drivers were partly trait-specific and thus complementary, yet, not interactive. Strikingly, effects on FD were evident despite accounting for changes in pollinator richness in all models. Furthermore, changes in pollinator richness were neither related to natural habitat loss nor to relative exotic abundance. Thus pollinator richness was a poor proxy of pollinator FD and may be insufficient when investigating changes in pollination processes. However, effects of the drivers can be trait-specific, which furthermore shows limited options to infer results for one functional trait from another. Overall, my results suggest that particularly specialized plants may suffer from reduced pollinator FD in habitats affected by habitat loss or plant invasion. In summary, understanding effects of natural habitat loss and exotic plant invasions on pollinator FD considerably benefits from separating FD measures into multivariate and univariate components, as well as from incorporating multiple drivers of global change.

Third, across nine study sites that differed in their degree of natural habitat loss and relative abundance of invasive exotic plant species, I investigated interactions between plants and their frugivores. I thereby focused on understanding whether changes in the structure of plant–frugivore interaction networks were driven by guild-specific responses of frugivores to habitat loss or plant invasion. I classified frugivores into functional guilds based on their degree of forest dependency and on their degree of frugivory. I used visitation rates as a measure of the relative importance of different frugivore guilds for frugivory (and thus potentially seed dispersal) of plant species, and investigated whether visitation changed guild-specifically with increasing habitat loss and relative invasive plant abundance. I assumed that generalist frugivores with low forest dependency or generalized fruit choice would be less affected by the two drivers as compared to forest specialists and specialized frugivores. Furthermore, I expected that synergistic effects between the two drivers would negatively affect specialized frugivores. I found that forest dependency and the degree of frugivory predicted the response of frugivores to natural habitat loss and exotic plant invasions. Furthermore, natural habitat loss and exotic plant invasion affected frugivores via different response traits, with habitat loss affecting

frugivores via species-specific differences in forest dependency and plant invasion affecting frugivores via species-specific differences in degree of frugivory. Overall, visitation rates of generalist frugivores, i.e. frugivores with low forest dependency or obligate frugivores with a generalized fruit choice, were unaffected by the two drivers. Thus, forest generalists and obligate frugivores may play a key-role for forest regeneration in degraded forest landscapes. As the composition of functional guilds of frugivores was similar between native and exotic plants, especially generalist frugivores may promote the spread and the integration of exotic plants into native plant–frugivore food webs. In contrast, lower visitation rates of forest specialists and frugivores with specialized fruit choice indicate the loss of their potentially complementary contributions to seed dispersal in degraded forest landscapes, which may have profound effects on patterns in forest regeneration. Importantly, I found that especially partial frugivores with a specialized fruit choice were negatively affected by synergistic effects between habitat loss and plant invasion. This finding confirms the prediction of a positive relationship between the specialization of species and their vulnerability to interactive effects of different drivers of global change.

In conclusion, the studies presented in this thesis demonstrate that natural habitat loss and exotic plant invasions profoundly alter and partly disrupt plant–animal mutualistic interactions. Specialized species and interactions are especially vulnerable, which may not only affect their own survival but also that of their mutualistic partners. Here, it should be noted that my findings indicate that both studied mutualisms, pollination and seed dispersal, are equally likely to be significantly altered by global change, despite marked differences between them such as the specialization between mutualistic partners. Furthermore, the community approach applied in all of my studies showed that the overall effects of the two global change drivers on the studied mutualism are generally negative, but also allowed me to separate the responses of different species to the two drivers. Here, I showed that these responses were in many cases directly related to the functional traits of species. In contrast, species richness was a poor representative of changes in the functional composition of species communities. Consequently, understanding and predicting ecological processes under global change considerably benefits from functional trait-based approaches. Furthermore, I found that different drivers of global change affect communities via different response traits. Results obtained from one functional trait therefore may not be representative for those from another trait.

Similarly, in all of my studies I found marked effects of the two investigated global change drivers on mutualistic interactions and the composition of species communities. However, effects were often specific to one driver, and many results would have been overlooked in single-driver studies. Consequently, my results highlight the need to include multiple global change drivers when studying ecosystem processes on a community scale. Here, I found that the two drivers can be complementary in their negative effects on specialized species and interactions. While these additive effects are already worrying, I also found evidence for negative synergistic effects between the two drivers on specialized species. Such synergisms considerably increase the risk of species' extinctions and thus of a permanent disruption of essential ecosystem processes.

We are living on a human-dominated planet. Understanding how global change affects ecosystem functioning and related ecosystem services remains an important challenge for scientists worldwide, yet, our knowledge is increasing. The loss of specialized species, specialized interactions and functional diversity within species communities as demonstrated in this thesis directly corresponds to the mounting evidence that ongoing global change may well jeopardize the functioning of many of the world's ecosystems. Major challenges ahead are the improvement of predictions of the consequences of the observed changes across ecosystems, as well as the development of sustainable management practices and, where applicable, restoration measures.

6 Future research perspectives

In the present thesis, I estimated changes in pollination and seed dispersal processes with natural habitat loss and exotic plant invasions from field data on flower visitation rates of insects and fruit consumption of frugivorous birds. A necessary next step is to assess whether the detected changes in visitation rates, fruit consumption and specialization of plant–animal mutualistic interactions also translate into reduced reproductive output of plant species or to different patterns in seed dispersal. Flower visitors and frugivores greatly differ in their pollination and seed dispersal effectiveness, respectively (Ne'eman et al. 2010; Schupp et al. 2010). Consequently, the functional differences of plant and animal species are important predictors of pollination and seed dispersal processes, which require further investigation. In addition to approaches investigating the functional roles of species, phylogenetic analyses comprise promising tools for assessing the role of interspecific diversity for community productivity and stability. For example, recently, high phylogenetic diversity of plant communities has been shown to increase plant biomass production (Cadotte 2013). It would be highly interesting to investigate a similar link between the phylogenetic diversity of animal mutualistic communities and the reproductive output as well as patterns in seed dispersal of their respective plant partners.

Furthermore, here I focused on two very important drivers of global change in subtropical and tropical ecosystems – natural habitat loss and exotic plant invasions. However, other drivers may also be important for the structure of ecosystems and ecosystem processes. Climate change, or more specifically global warming, may increase rates of exotic plant invasions, although most predictions are still highly uncertain and vary considerably across the investigated species and ecosystems (Bradley et al. 2010). For plant–animal mutualisms, particularly the identification of non-additive, e.g. synergistic, effects between climate change, exotic plant invasions and natural habitat loss remains an important challenge (González-Varo et al. 2013).

Finally, in the present thesis I investigated naturally occurring plant–pollinator communities in a heterogeneous landscape. This is an appropriate approach when the aim is to understand consequences of global change for real-world ecosystems. However, when the intention is to investigate effects associated with specific changes in the structure of plant–animal interaction networks, experimental settings with artificial plant–pollinator communities may be more appropriate. For example, Fontaine et al. (2006) used experimental communities to manipulate the functional group composition of plants and pollinators. The authors found that high pollinator FD led to the recruitment of more

diverse plant communities, and that functional complementarity among plants and pollinators enhanced the stability of the overall plant–pollinator community. Future studies could set up artificial plant mesocosms along environmental gradients (e.g. land-use intensity), and evaluate whether the naturally occurring pollinator community is able to maintain the reproductive output of these plant species and the stability of the overall plant–pollinator community. Such an approach could especially help to identify the most vulnerable animal-pollinated plant species and plant–pollinator interactions to global change.

7 Deutsche Zusammenfassung

Habitatverlust und Invasionen gebietsfremder, exotischer Pflanzenarten sind zwei hauptverantwortliche Treiber des globalen Wandels. Diese Treiber bedrohen sowohl natürliche Artengemeinschaften als auch essentielle Ökosystemprozesse, wie beispielsweise die Bestäubung und Samenausbreitung von Pflanzenarten durch Tierarten. In subtropischen und tropischen Wäldern sind bis zu 90% aller Pflanzenarten auf die Bestäubung durch Tiere sowie die Samenausbreitung durch Frugivore angewiesen. Insbesondere spezialisierte Pflanze-Tier Interaktionen könnten durch den Verlust natürlicher Habitate und Pflanzeninvasionen bedroht sein. Ebenso könnte ein Verlust der funktionellen Diversität von Artengemeinschaften durch die beiden Treiber eine Reduktion der Funktionsfähigkeit von Ökosystemen in degradierten Habitaten anzeigen. Dennoch sind die Auswirkungen von Habitatverlust und Pflanzeninvasionen auf Bestäubungs- und Samenausbreitungsprozesse bisher wenig verstanden. In einer heterogenen, subtropischen Waldlandschaft in Südafrika untersuchte ich den Einfluss des Verlusts natürlicher Habitate und der relativen Abundanz exotischer Pflanzenarten auf Pflanze-Bestäuber Interaktionen, die funktionelle Diversität von Bestäubergemeinschaften und Pflanze-Frugivor Interaktionen. In einer ersten Studie fand ich eine Verringerung der Spezialisierung von Pflanze-Bestäuber Interaktionen, welche auf einen Verlust spezialisierter Interaktionen mit zunehmendem Habitatverlust und zunehmendem Anteil exotischer Pflanzenarten hinwies. Dieser Verlust wurde von einer Änderung der Zusammensetzung der Bestäubergemeinschaften in Richtung eines höheren Anteils an Habitatgeneralisten begleitet. In einer zweiten Studie fand ich eine Verringerung der funktionellen Diversität der Bestäubergemeinschaften in verschiedenen morphologischen Merkmalen mit zunehmendem Habitatverlust sowie zunehmendem Anteil exotischer Pflanzenarten in meinen Untersuchungsflächen. Hierbei hatten Habitatverlust und Pflanzeninvasionen teils merkmalspezifische und teils vergleichbare negative Effekte auf die funktionelle Diversität der Bestäubergemeinschaften. Trotz der Abnahme der funktionellen Diversität fand ich keine gerichtete Veränderung in der Artenzahl von Bestäubern mit zunehmendem Habitatverlust oder zunehmendem Anteil exotischer Pflanzenarten. Die Artenzahl der Bestäubergemeinschaften war somit ein schlechter Indikator ihrer funktionellen Diversität. In einer dritten Studie fand ich Änderungen in Pflanze-Frugivor Interaktionen mit zunehmendem Habitatverlust und Invasionsgrad meiner Untersuchungsflächen. Hierbei waren die Besuchsmuster von Habitatgeneralisten und obligaten Frugivoren mit einem generalisierten Nahrungsspektrum jeweils wenig von

Habitatverlust und Pflanzeninvasionen betroffen. Jedoch nahmen die Besuchsraten von Frugivoren mit einer hohen Spezialisierung auf natürliche Wälder oder einer Spezialisierung auf bestimmte fruchtende Pflanzenarten mit zunehmendem Habitatverlust und Invasionsgrad ab. Dabei bewirkten insbesondere negative, synergistische Effekte zwischen Habitatverlust und Invasionsgrad eine Abnahme der Besuchsrate von spezialisierten, partiellen Frugivoren. Zudem hingen Veränderungen der Besuchsraten mit Habitatverlust von der Waldspezialisierung der Frugivore ab, während Veränderungen mit zunehmenden Invasionsgrad der Untersuchungsflächen von der Spezialisierung der Frugivore auf fleischige Früchte abhingen. Zusammenfassend zeigen diese drei Studien, dass der Verlust natürlicher Habitate und Invasionen exotischer Pflanzenarten insbesondere spezialisierte Pflanze-Tier Interaktionen negativ beeinflussen. Ebenso kann es zu einem Verlust von funktioneller Diversität kommen, welcher bei einem ausschließlichen Fokus auf Artenzahlen nicht zum Vorschein tritt. Habitatverlust und Pflanzeninvasionen haben vergleichbare negative Effekte auf Pflanze-Tier Mutualismen. Jedoch hängen die Reaktionen einzelner Tierarten auf diese beiden Treiber des globalen Wandels von artspezifischen Merkmalen, wie beispielsweise ihrer Habitatspezialisierung oder bestimmten morphologischen Merkmalen, ab. Die Erforschung der Effekte des globalen Wandels auf natürliche Ökosystemprozesse profitiert daher von integrierten Ansätzen, welche mehrere Treiber umfassen und einen Fokus auf mehrere funktionelle Merkmale von Arten legen.

8 Appendix

Please note that the figure and table numeration
in the appendices follows the numeration used in chapters 2–4
(e.g. Fig. S2.1 corresponds to the first supplementary figure of chapter 2)

Appendix chapter 2

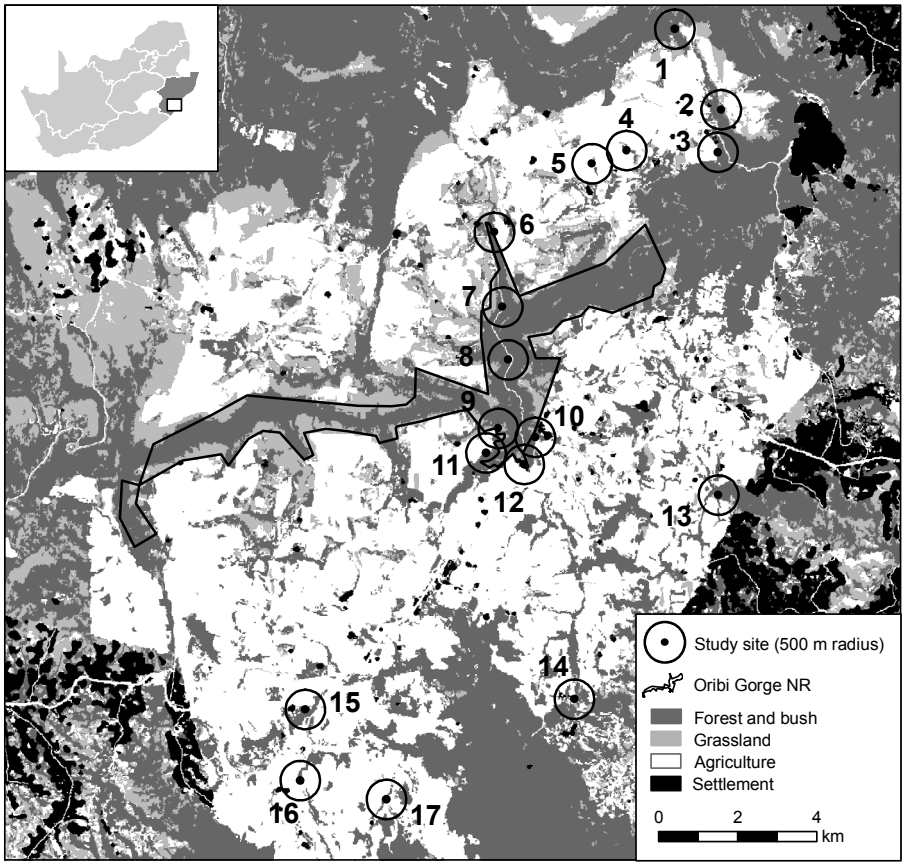

Fig. S2.1 Map of the study area showing the location of the 17 study sites. Circles surrounding the center of study sites refer to the 500 m radius used for analysis on land-use intensity. The black line shows the border of Oribi Gorge Nature Reserve. Natural habitats such as forest or bush and grassland are shaded in dark and light grey, respectively. Habitats for agricultural use (particularly sugarcane farming) are shown in white, areas with urban or rural settlements are shown in black. For visual clarity, roads are not shown in black but in white. See Table S2.1 for geographical coordinates of study sites and information on relative abundance of exotic plants and land-use intensity.

Table S2.1 Universal Transverse Mercator (UTM) coordinates and altitude of study sites, as well as mean exotic and total floral abundance (measured in floral units [FU]) across transects over the study period, relative exotic abundance and land-use intensity. In statistical analyses, relative exotic abundance was sqrt-transformed, here raw values are presented. Numbers of study sites refer to those used on the map of the study area (Fig. S2.1)

No of study site	UTM coordinates	Altitude [m]	Exotic floral abundance [FU]	Total floral abundance [FU]	Relative exotic abundance	Land-use intensity
1	36 J 242569 6608036	265	466	661	0.70	0.16
2	36 J 243778 6606013	400	440	769	0.57	0.46
3	36 J 243714 6604931	397	1109	1520	0.73	0.38
4	36 J 241404 6604934	421	1553	4700	0.33	0.90
5	36 J 240540 6604584	422	220	5392	0.041	0.96
6	36 J 238096 6602799	491	1320	2223	0.59	0.42
7	36 J 238339 6600909	291	1082	1114	0.97	0.085
8	36 J 238503 6599569	215	723	890	0.81	0.041
9	36 J 238283 6597826	403	84	369	0.23	0.14
10	36 J 239226 6597618	506	215	1313	0.16	0.43
11	36 J 237984 6597197	432	476	1871	0.26	0.450
12	36 J 238957 6596925	460	0	244	0.00	0.60
13	36 J 243887 6596234	295	335	1382	0.24	0.48
14	36 J 240332 6590993	438	73	1617	0.045	0.42
15	36 J 233531 6590610	541	1445	4569	0.32	0.62
16	36 J 233434 6588803	507	516	1160	0.45	0.91
17	36 J 235624 6588363	488	265	1427	0.19	0.80

Table S2.2 List of observed plant species during the study, sorted by study site, origin of plant species and scientific name. Number of study sites refers to the numbers used on the map of the study area (Fig. S2.1). Plant codes correspond to the codes used in raw data matrices. Given are the scientific name of plant species, plant family and origin of plant species. See manuscript for methods on calculation of specialization (*d'*) of plant species and weighted mean of pollinators on plant species. Plant linkage level was defined as the number of visits per plant species divided by plant species richness in a given study site (Vilà et al. 2009). Given are the mean number of observed floral units of a focal plant species over the four observations sessions (totaling 80 min of observation) and the focal species' mean total abundance in the transect during the observations. The second to last column shows the mean total floral abundance of all flowering plant species during the observation sessions of a focal plant species, and was used to calculate the relative abundance of the plant species in relation to the total floral abundance of all plant species in a study site. Species identification and species names followed Pooley (1998) and Boon (2010). Origin of plant species was determined according to Pooley (1998) and Henderson (2007).

Study site	Plant code	Plant species	Plant Family	Origin	Plant *d'*	Pollinator *d'*	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
1	AnAe	*Aneilema aequinoctiale*	Commelinaceae	native	0.61	0.31	8	1.14	40	50	800	0.06
1	CrEx	*Crassula expansa ssp. fragilis*	Crassulaceae	native	0.00	0.47	1	0.14	9	10	106	0.09
1	MiMe	*Microglossa mespilifolia*	Asteraceae	native	0.67	0.28	10	1.43	72	253	1498	0.17
1	SeMa	*Senecio madagascariensis*	Asteraceae	native	0.51	0.32	5	0.71	29	138	1639	0.08
1	BiPi	*Bidens pilosa*	Asteraceae	exotic	1.00	1.00	1	0.14	36	70	941	0.07
1	LaCa	*Lantana camara*	Verbenaceae	exotic	0.80	0.26	9	1.29	64	1275	1840	0.69
1	SoMa	*Solanum mauritianum*	Solanaceae	exotic	1.00	1.00	1	0.14	13	31	677	0.05
2	AsGa	*Asystasia gangetica*	Acanthaceae	native	1.00	0.38	7	1.17	8	9	144	0.06
2	BuBu	*Burchellia bubalina*	Rubiaceae	native	0.66	0.50	5	0.83	17	185	1539	0.12

Study site	Plant code	Plant species	Plant Family	Origin	Plant *d'*	Pollinator *d'*	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
2	HeCe	*Helichrysum cephaloideum*	Asteraceae	native	NA	NA	0	0.00	7	17	150	0.11
2	PiVi	*Pittosporum viridiflorum*	Pittosporaceae	native	0.80	0.43	14	2.33	23	325	1376	0.24
2	SeMa	*Senecio madagascariensis*	Asteraceae	native	1.00	0.68	8	1.33	31	43	996	0.04
2	AcMe	*Acacia mearnsii*	Mimosaceae	exotic	1.00	0.74	2	0.33	12	450	938	0.48
2	LaCa	*Lantana camara*	Verbenaceae	exotic	1.00	1.00	3	0.50	34	83	1539	0.05
3	HeSp	*Helichrysum splendidum*	Asteraceae	native	0.39	0.25	28	4.67	91	379	2668	0.14
3	SePy	*Searsia pyroides*	Anacardiaceae	native	0.82	0.35	16	2.67	19	900	2216	0.41
3	SeMa	*Senecio madagascariensis*	Asteraceae	native	0.58	0.20	18	3.00	18	26	1966	0.01
3	SePo	*Senecio polyanthemoides*	Asteraceae	native	0.51	0.23	21	3.50	13	45	2363	0.02
3	AcMe	*Acacia mearnsii*	Mimosaceae	exotic	0.51	0.47	10	1.67	20	1000	2363	0.42
3	LaCa	*Lantana camara*	Verbenaceae	exotic	0.72	0.46	12	2.00	100	745	2344	0.32
4	AsGa	*Asystasia gangetica*	Acanthaceae	native	0.34	0.21	6	0.60	26	56	2220	0.03
4	CrEx	*Crassula expansa ssp. fragilis*	Crassulaceae	native	0.91	0.79	3	0.30	20	31	2133	0.02

Study site	Plant code	Plant species	Plant Family	Origin	Plant d'	Pollinator d'	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
4	HeRu	*Helichrysum ruderale*	Asteraceae	native	0.59	0.31	19	1.90	26	65	3806	0.02
4	HeSp	*Helichrysum splendidum*	Asteraceae	native	0.24	0.24	29	2.90	61	1988	7375	0.27
4	IpCa	*Ipomoea cairica*	Convolvulaceae	native	0.24	0.41	3	0.30	4	7	2220	0.00
4	SeMa	*Senecio madagascariensis*	Asteraceae	native	0.34	0.27	26	2.60	173	3598	8951	0.40
4	SePo	*Senecio polyanthemoides*	Asteraceae	native	0.18	0.23	11	1.10	25	1100	5160	0.21
4	AcMe	*Acacia mearnsii*	Mimosaceae	exotic	NA	NA	0	0.00	9	140	5160	0.03
4	AgCo	*Ageratum conyzoides*	Asteraceae	exotic	0.84	0.82	2	0.20	61	170	9530	0.02
4	BiPi	*Bidens pilosa*	Asteraceae	exotic	0.53	0.31	8	0.80	23	115	6378	0.02
4	LaCa	*Lantana camara*	Verbenaceae	exotic	0.37	0.33	3	0.30	93	1398	5072	0.28
5	BrMi	*Bridelia micrantha*	Euphorbiaceae	native	0.92	0.82	10	0.71	15	2450	4731	0.52
5	CrEx	*Crassula expansa ssp. fragilis*	Crassulaceae	native	0.83	0.55	2	0.14	20	36	5804	0.01
5	GoPh	*Gomphocarpus physocarpus*	Asclepiadaceae	native	0.83	0.47	8	0.57	9	50	8396	0.01
5	HeRu	*Helichrysum ruderale*	Asteraceae	native	0.54	0.32	10	0.71	20	2555	8555	0.30
5	HeSp	*Helichrysum splendidum*	Asteraceae	native	0.00	0.37	1	0.07	28	38	7885	0.01

Study site	Plant code	Plant species	Plant Family	Origin	Plant *d'*	Pollinator *d'*	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
5	HyAn	*Hypoxis angustifolia*	Hypoxidaceae	native	0.52	0.39	9	0.64	23	34	8555	0.00
5	MaLa	*Maesa lanceolata*	Myrsinaceae	native	0.64	0.36	12	0.86	51	1998	3434	0.58
5	MoSt	*Monopsis stellarioides*	Lobeliaceae	native	0.81	0.61	5	0.36	14	21	6467	0.00
5	SePy	*Searsia pyroides*	Anacardiaceae	native	0.56	0.31	15	1.07	12	4000	8396	0.48
5	SeMa	*Senecio madagascariensis*	Asteraceae	native	0.36	0.32	18	1.29	133	1248	4941	0.25
5	SePo	*Senecio polyanthemoides*	Asteraceae	native	0.50	0.35	43	3.07	14	1055	5436	0.19
5	BiPi	*Bidens pilosa*	Asteraceae	exotic	0.39	0.36	2	0.14	20	41	5804	0.01
5	LaCa	*Lantana camara*	Verbenaceae	exotic	1.00	1.00	1	0.07	18	80	5277	0.02
5	VeBo	*Verbena bonariensis*	Verbenaceae	exotic	0.83	0.46	20	1.43	25	65	8237	0.01
6	BrMi	*Bridelia micrantha*	Euphorbiaceae	native	0.72	0.61	39	4.88	73	700	1286	0.54
6	CaTi	*Cassinopsis tinifolia*	Icacinaceae	native	0.53	0.50	8	1.00	26	120	1286	0.09
6	HeSp	*Helichrysum splendidum*	Asteraceae	native	0.75	0.32	23	2.88	188	1075	3836	0.28
6	MiMe	*Microglossa mespilifolia*	Asteraceae	native	0.22	0.59	6	0.75	61	344	4358	0.08
6	SeMa	*Senecio madagascariensis*	Asteraceae	native	0.82	0.54	5	0.63	25	72	1575	0.05

Study site	Plant code	Plant species	Plant Family	Origin	Plant *d'*	Pollinator *d'*	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
6	AcMe	*Acacia mearnsii*	Mimosaceae	exotic	0.82	0.46	23	2.88	43	1275	3041	0.42
6	AgCo	*Ageratum conyzoides*	Asteraceae	exotic	1.00	0.81	2	0.25	66	328	4110	0.08
6	LaCa	*Lantana camara*	Verbenaceae	exotic	1.00	0.81	2	0.25	58	565	1575	0.36
7	GrOc	*Grewia occidentalis*	Tiliaceae	native	NA	NA	0	0.00	4	9	1251	0.01
7	MiMe	*Microglossa mespilifolia*	Asteraceae	native	1.00	0.51	4	0.67	8	40	581	0.07
7	SeMa	*Senecio madagascariensis*	Asteraceae	native	0.56	0.31	4	0.67	10	15	1309	0.01
7	ThDr	*Thunbergia cf. dregeana*	Acanthaceae	native	1.00	0.52	3	0.50	8	16	581	0.03
7	BiPi	*Bidens pilosa*	Asteraceae	exotic	0.39	0.46	2	0.33	8	9	1660	0.01
7	GaPa	*Galinsoga parviflora*	Asteraceae	exotic	1.00	0.69	3	0.50	190	965	1131	0.85
7	OxCo	*Oxalis corniculata*	Oxalidaceae	exotic	0.52	0.05	10	1.67	33	120	1136	0.11
8	CoEr	*Commelina erecta*	Commelinaceae	native	0.86	0.75	2	0.22	3	4	290	0.01
8	EuCh	*Euryops chrysanthemoides*	Asteraceae	native	0.29	0.57	10	1.11	18	64	2123	0.03
8	SeMa	*Senecio madagascariensis*	Asteraceae	native	0.66	0.80	8	0.89	23	90	818	0.11

Study site	Plant code	Plant species	Plant Family	Origin	Plant *d'*	Pollinator *d'*	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
8	StAe	*Stachys cf. aethiopica*	Lamiaceae	native	0.89	0.56	3	0.33	17	45	1628	0.03
8	AgCo	*Ageratum conyzoides*	Asteraceae	exotic	0.82	0.32	18	2.00	103	2103	2123	0.99
8	LaCa	*Lantana camara*	Verbenaceae	exotic	0.93	0.56	6	0.67	14	38	1098	0.03
8	OpSt	*Opuntia stricta*	Cactaceae	exotic	0.71	0.40	3	0.33	2	7	318	0.02
8	VeAr	*Verbena aristigera*	Verbenaceae	exotic	0.86	0.75	2	0.22	24	44	800	0.06
9	DaOb	*Dalbergia obovata*	Fabaceae	native	0.66	0.20	22	4.40	19	95	349	0.27
9	EkPt	*Ekebergia pterophylla*	Meliaceae	native	0.66	0.24	13	2.60	43	440	527	0.84
9	NeCa	*Nectaropetalum capense*	Erythroxylaceae	native	NA	NA	0	0.00	14	18	527	0.03
9	OlHe	*Oldenlandia herbacea*	Rubiaceae	native	1.00	0.50	7	1.40	18	50	253	0.20
9	PoPu	*Polystachya pubescens*	Orchidaceae	native	NA	NA	0	0.00	15	17	257	0.06
9	StPo	*Streptocarpus polyanthus*	Gesneriaceae	native	1.00	1.00	1	0.20	5	8	323	0.02
9	SeBi	*Senna bicapsularis*	Caesalpiniaceae	exotic	0.66	0.57	4	0.80	10	36	323	0.11
10	BuBu	*Burchellia bubalina*	Rubiaceae	native	0.60	0.56	25	5.00	14	63	1760	0.04

Study site	Plant code	Plant species	Plant Family	Origin	Plant d'	Pollinator d'	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
10	HeSp	*Helichrysum splendidum*	Asteraceae	native	0.33	0.50	7	1.40	53	1053	3430	0.31
10	MoUn	*Monopsis unidentata*	Lobeliaceae	native	0.82	0.71	2	0.40	11	27	77	0.35
10	PsCa	*Psychotria capensis*	Rubiaceae	native	0.61	0.42	20	4.00	44	2155	4190	0.51
10	AgCo	*Ageratum conyzoides*	Asteraceae	exotic	0.60	0.43	12	2.40	69	448	3430	0.13
11	HeSp	*Helichrysum splendidum*	Asteraceae	native	0.91	0.31	16	4.00	75	3805	4582	0.83
11	SeMa	*Senecio madagascariensis*	Asteraceae	native	1.00	0.42	14	3.50	7	13	2475	0.01
11	AcMe	*Acacia mearnsii*	Mimosaceae	exotic	0.69	0.65	5	1.25	15	310	2703	0.12
11	LaCa	*Lantana camara*	Verbenaceae	exotic	1.00	0.62	4	1.00	47	256	2829	0.09
12	BuBu	*Burchellia bubalina*	Rubiaceae	native	0.80	0.72	31	5.17	13	260	279	0.93
12	CaTi	*Cassinopsis tinifolia*	Icacinaceae	native	0.87	0.49	8	1.33	40	140	279	0.50
12	CoEr	*Commelina erecta*	Commelinaceae	native	NA	NA	0	0.00	17	24	193	0.12
12	ErPi	*Erythroxylum pictum*	Erythroxylaceae	native	NA	NA	0	0.00	7	20	242	0.08
12	GyHe	*Gymnosporia heterophylla*	Celastraceae	native	0.64	0.37	49	8.17	35	85	151	0.56

Study site	Plant code	Plant species	Plant Family	Origin	Plant *d'*	Pollinator *d'*	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
12	PsCa	*Psychotria capensis*	Rubiaceae	native	1.00	0.72	3	0.50	15	19	279	0.07
12	StAe	*Stachys cf. aethiopica*	Lamiaceae	native	1.00	0.82	2	0.33	6	13	264	0.05
12	TrDi	*Tritonia disticha*	Iridaceae	native	1.00	1.00	1	0.17	4	4	273	0.02
13	BuBu	*Burchellia bubalina*	Rubiaceae	native	1.00	0.90	10	0.91	23	210	1831	0.12
13	HeSp	*Helichrysum splendidum*	Asteraceae	native	0.41	0.33	22	2.00	53	550	3784	0.15
13	KeGu	*Keetia gueinzii*	Rubiaceae	native	0.35	0.36	8	0.73	12	120	767	0.16
13	SelDen	*Selago densiflora*	Scrophulariaceae	native	0.74	0.34	11	1.00	70	310	3616	0.09
13	SePo	*Senecio polyanthemoides*	Asteraceae	native	0.64	0.38	35	3.18	24	1529	3287	0.47
13	SiCo	*Sida cordifolia*	Malvaceae	native	NA	NA	0	0.00	3	9	359	0.02
13	TeGr	*Tephrosia grandiflora*	Fabaceae	native	0.69	0.64	4	0.36	38	610	3281	0.19
13	TrDi	*Tritonia disticha*	Iridaceae	native	NA	NA	0	0.00	3	3	3616	0.00
13	AgCo	*Ageratum conyzoides*	Asteraceae	exotic	0.40	0.33	5	0.46	59	360	3616	0.10
13	LaCa	*Lantana camara*	Verbenaceae	exotic	0.50	0.39	8	0.73	48	220	3294	0.07
13	RiBr	*Richardia brasiliensis*	Rubiaceae	exotic	1.00	1.00	2	0.18	26	88	3294	0.03

Study site	Plant code	Plant species	Plant Family	Origin	Plant *d'*	Pollinator *d'*	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
13	RuCu	*Rubus cuneifolius*	Rosaceae	exotic	0.26	0.34	11	1.00	14	115	1831	0.06
14	BuBu	*Burchellia bubalina*	Rubiaceae	native	0.88	0.58	2	0.20	11	56	2734	0.02
14	CoEr	*Commelina erecta*	Commelinaceae	native	NA	NA	0	0.00	10	40	420	0.10
14	CoNa	*Conostomium natalense*	Rubiaceae	native	0.88	0.65	2	0.20	28	56	487	0.12
14	CrEx	*Crassula expansa ssp. fragilis*	Crassulaceae	native	0.92	0.78	4	0.40	33	60	815	0.07
14	HeSp	*Helichrysum splendidum*	Asteraceae	native	0.53	0.50	22	2.20	59	973	3524	0.28
14	KeGu	*Keetia gueinzii*	Rubiaceae	native	0.82	0.43	4	0.40	6	447	2095	0.21
14	LoAn	*Lobelia anceps*	Lobeliaceae	native	1.00	1.00	1	0.10	30	40	297	0.14
14	SelDen	*Selago densiflora*	Scrophulariaceae	native	0.77	0.45	10	1.00	47	120	3331	0.04
14	SePo	*Senecio polyanthemoides*	Asteraceae	native	0.38	0.39	22	2.20	25	2113	3384	0.62
14	SiCo	*Sida cordifolia*	Malvaceae	native	1.00	1.00	1	0.10	3	6	359	0.02
14	LaCa	*Lantana camara*	Verbenaceae	exotic	1.00	1.00	1	0.10	12	23	2734	0.01
15	GoPh	*Gomphocarpus physocarpus*	Asclepiadaceae	native	0.75	0.60	8	0.80	7	8	3602	0.00

Study site	Plant code	Plant species	Plant Family	Origin	Plant *d'*	Pollinator *d'*	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
15	HeRu	*Helichrysum ruderale*	Asteraceae	native	0.74	0.40	8	0.80	18	65	3348	0.02
15	HeSp	*Helichrysum splendidum*	Asteraceae	native	0.45	0.27	46	4.60	120	666	7140	0.09
15	SeDe	*Searsia dentata*	Anacardiaceae	native	0.61	0.24	38	3.80	69	2325	7974	0.29
15	SeMa	*Senecio madagascariensis*	Asteraceae	native	1.00	0.43	17	1.70	15	21	2153	0.01
15	SePo	*Senecio polyanthemoides*	Asteraceae	native	0.25	0.27	33	3.30	26	380	6087	0.06
15	TrOr	*Trema orientalis*	Celtidaceae	native	NA	NA	0	0.00	35	1400	2308	0.61
15	AcMe	*Acacia mearnsii*	Mimosaceae	exotic	0.37	0.42	5	0.50	41	3475	7974	0.44
15	AgCo	*Ageratum conyzoides*	Asteraceae	exotic	1.00	1.00	1	0.10	53	110	7698	0.01
15	LaCa	*Lantana camara*	Verbenaceae	exotic	0.13	0.31	2	0.20	58	168	5396	0.03
15	SoMa	*Solanum mauritianum*	Solanaceae	exotic	0.41	0.36	3	0.30	9	86	7974	0.01
16	CoEr	*Commelina erecta*	Commelinaceae	native	NA	NA	0	0.00	6	14	1817	0.01
16	CoNa	*Conostomium natalense*	Rubiaceae	native	NA	NA	0	0.00	5	6	1896	0.00
16	HeRu	*Helichrysum ruderale*	Asteraceae	native	0.27	0.39	4	0.80	31	198	1375	0.14
16	HeSp	*Helichrysum splendidum*	Asteraceae	native	0.58	0.32	40	8.00	66	1090	2166	0.50

Study site	Plant code	Plant species	Plant Family	Origin	Plant *d'*	Pollinator *d'*	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
16	KeGu	*Keetia gueinzii*	Rubiaceae	native	0.57	0.37	63	12.60	6	96	716	0.13
16	SePo	*Senecio polyanthemoides*	Asteraceae	native	0.36	0.36	14	2.80	10	173	1375	0.13
16	AgCo	*Ageratum conyzoides*	Asteraceae	exotic	NA	NA	0	0.00	52	85	1993	0.04
16	LaCa	*Lantana camara*	Verbenaceae	exotic	0.89	0.61	2	0.40	31	496	1993	0.25
17	CoEr	*Commelina erecta*	Commelinaceae	native	0.79	0.65	2	0.18	10	25	1490	0.02
17	HeRu	*Helichrysum ruderale*	Asteraceae	native	0.02	0.63	11	1.00	26	585	2029	0.29
17	KeGu	*Keetia gueinzii*	Rubiaceae	native	0.08	0.63	26	2.36	5	540	2294	0.24
17	LuOc	*Ludwigia octovalvis*	Onagraceae	native	0.08	0.60	8	0.73	12	143	1455	0.10
17	SeMa	*Senecio madagascariensis*	Asteraceae	native	0.68	0.43	8	0.73	46	375	940	0.40
17	SyCo	*Syzigium cordatum*	Myrtaceae	native	0.18	0.51	18	1.64	6	450	2003	0.23
17	AgCo	*Ageratum conyzoides*	Asteraceae	exotic	1.00	1.00	1	0.09	29	100	1385	0.07
17	BiPi	*Bidens pilosa*	Asteraceae	exotic	0.00	0.63	1	0.09	9	18	2003	0.01
17	LaCa	*Lantana camara*	Verbenaceae	exotic	1.00	0.69	4	0.36	59	90	2533	0.04
17	RuCu	*Rubus cuneifolius*	Rosaceae	exotic	0.09	0.63	29	2.64	14	80	1455	0.06

Study site	Plant code	Plant species	Plant Family	Origin	Plant *d'*	Pollinator *d'*	Visitation rate	Plant linkage level	FU observed (focal species)	FU transect (focal species)	FU transect (all species)	Relative abundance plant species
17	VeBr	*Verbena brasiliensis*	Verbenaceae	exotic	0.85	0.54	4	0.36	45	63	2533	0.03

Table S2.3 Detailed information on the abundance of plants recorded during the transect walks at each study site. Species' abundances were estimated by the mean number of floral units over all transect walks. Abundances of plants species chosen for pollinator observations are shown in bold, abundances of species recorded in transect walks but not observed are shown in regular font. Number of study sites refers to the numbers used on the map of the study area (Fig S2.1). Plant codes correspond to the codes used in Table S2.2, which holds information on species names and specialization. Due to unstable weather conditions, not all flowering plant species could be observed, and completeness of sampling varies across study sites. Completeness of sampling is shown at the end of the table, with information on observed and total plant richness across transects, and the respective floral abundance of observed and all recorded plant species during transects walks in floral units (FU). Species identification followed Pooley (1998) and Boon (2010), origin of plant species was determined according to Pooley (1998) and Henderson (2007). For plant species which could not be identified to species level, no origin is given.

	Study site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Plant code	**Origin**																	
AcMe	exotic		**317.9**	**55.0**	**78.8**		**768.3**					**189.3**		28.9	5.0	**1154.4**		
AgCo	exotic		1.6		**42.5**		**132.5**	5.7	**652.8**		**215.0**			**117.7**		**35.0**	**37.2**	**45.5**
AnAe	native	**14.5**																
ArAb	native												1.7					
AsGa	native		**2.4**		**25.0**													
BiPi	exotic	**56.9**	0.1		**82.5**	**27.1**	1.0	**9.3**	0.6					1.0		1.6		**18.0**
BrMi	native					**825.0**	**141.7**											
BuBu	native		**13.0**								**46.3**		**129.7**	**65.7**	**26.3**			
CaTi	native						**26.7**						**34.3**					
CoAf	native												0.9					
CoEr	native				0.4			0.3	**1.0**				**9.3**		**12.5**		**5.6**	**8.0**
CoNa	native						**0.8**								**31.4**		**4.2**	
CrEx	native	**2.4**			**24.4**	**13.8**									**17.5**			0.3
DaOb	native									**27.1**								
DiGr	native								0.6					0.2				
EkPt	native									**194.3**								
ErPi	native												**5.7**					
EuCh	native								**15.5**									
GaPa	exotic							**99.0**										
Ge sp	NA													**5.0**				
GoPh	native					**17.9**										**4.3**		
GrOc	native							**9.9**										

	Study site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Plant code	**Origin**																	
GyHe	native												**37.9**					
HaLu	native				8.8	268.8											62.2	
HeCe	native		**6.1**															
HeRu	native				**41.9**	**1325.6**								2.9	5.6	**35.8**	**128.9**	**386.3**
HeSp	native		2.1	**173.0**	**995.6**	**17.5**	**498.3**				**38.0**	**1385.0**		137.8	**347.5**	**298.3**	**326.7**	
HyAn	native					**8.1**												
Hy sp	NA								**68.5**									
IpCa	native	0.8			**3.9**													
KeGu	native													**43.4**	**167.0**		**39.1**	**227.5**
LaCa	exotic	**4.0**	**12.9**	**64.3**	**1348.8**	**78.8**	**417.7**		**49.0**			**287.1**		**129.4**	**22.8**	**22.8**	**476.7**	**75.0**
LoAn	native														**1.0**			
LuOc	native																	**8.6**
MaLa	native					**393.8**							14.3				**1.1**	
MiMe	native	**8.0**					**15.0**	**8.6**										
MoSt	native					**5.6**												
MoUn	native										**5.0**							
NeCa	native									**5.0**								
OlHe	native									**24.3**								
OpSt	exotic								**1.5**									
OxCo	exotic							**77.1**										
PeAl	native								13.8									
PiVi	native		**184.3**															
Pl sp	exotic																	1.3
PoPu	native									**7.4**								
PsCa	native									16.4	**666.9**		**5.4**					
RiBr	exotic													**19.4**				
RuCu	exotic													**38.7**		8.1	0.8	**64.4**
SeBi	exotic									**83.6**								
SeDe	native															**12.0**		
SelDen	native													**111.1**	**65.0**			
SeMa	native	**96.9**	**31.0**	**12.3**	**1755.6**	**651.9**	**86.3**	**7.7**	**43.5**			**9.3**				**21.8**	0.3	**2.0**

	Study site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Plant code	**Origin**																	
SePo	native			**18.7**	**291.3**	**392.5**								**587.8**	**859.0**	**264.6**	**75.6**	21.3
SePy	native			**27.1**		**125.0**												
SiCo	native	0.6			0.6									**7.1**	**2.1**			1.3
SoMa	exotic	**8.6**														**33.7**	1.6	
So sp	NA	0.3																
StAe	native								**23.4**				**4.0**					
StPo	native									**11.1**								
SyCo	native					0.8								2.8				**235.6**
TeGr	native													**78.7**				1.9
ThAl	native													3.0				
ThDr	native							**5.0**										
TrDi	native												**0.6**	**1.1**				
TrOr	native															**13.0**		
VeAr	exotic								**19.4**									
VeBo	exotic					**114.5**												
VeBr	exotic																	**6.6**
ZaAe	native					0.4												
Plant richness observed		7	7	6	11	14	9	7	9	7	5	4	8	12	11	11	8	11
Plant richness in transect		10	10	6	14	17	10	9	12	8	5	4	11	19	13	13	13	16
Sampling completeness [%]		70	70	100	79	82	90	78	75	88	100	100	73	63	85	85	62	69
∑(FU of observed plants)		660	766	1520	4690	5122	2222	1108	875	353	1313	1871	227	1205	1561	4551	966	1402
∑(FU all plants in transects)		661	769	1520	4700	5392	2223	1114	890	369	1313	1871	244	1382	1617	4569	1160	1427
Sampling completeness [%]		100	99	100	100	95	100	99	98	96	100	100	93	87	97	100	83	98

Table S2.4 Taxonomic resolution of pollinator identification. Pollinators were identified to the lowest taxonomic level possible and afterwards sorted into morphospecies. Shown are the distribution and the number of observed individuals of the 139 morphospecies across the 17 study sites. Pollinator identification followed Picker et al. (2004), Woodhall (2005) and Scholtz and Holm (2008). Orders of pollinators (Col: Coleoptera; Dip: Diptera; Hym: Hymenoptera; Lep: Lepidoptera).

Study site	Animal code	Order	Family	Subfamily	Genus	Species	Indivi-duals
1	A21	Col	Scarabaeidae	Cetoniinae			1
	A34	Dip	Bombyliidae				1
	A42	Dip	Conopidae				4
	A48	Dip	Muscidae				1
	A65	Dip	Syrphidae				1
	A67	Dip	Syrphidae				6
	A68	Dip	Syrphidae				1
	A80	Hym	Anthophoridae				3
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	1
	A91	Hym	Colletidae				1
	A92	Hym	Colletidae				1
	A93	Hym	Eumenidae	Eumeninae	*Delta*	*emarginatum*	1
	A107	Hym	Halictidae				1
	A127	Lep	Nymphalidae	Heliconiinae	*Hyalites*	*esebria esebria*	1
	A134	Lep	Pieridae	Pierinae	*Belenois*	*gidica abyssinica*	3
	A135	Lep	Pieridae	Pierinae	*Belenois*	*zochalia zochalia*	1
	A137	Lep	Pieridae	Pierinae	*Colotis*	*ione*	1
	A138	Lep	Pieridae	Pierinae	*Dixeia*	*charina charina*	5
	A139	Lep					1
2	A8	Col	Chrysomelidae				1
	A9	Col	Chrysomelidae				1
	A21	Col	Scarabaeidae	Cetoniinae			6
	A23	Col	Scarabaeidae	Cetoniinae			3
	A42	Dip	Conopidae				2
	A63	Dip	Syrphidae				1
	A65	Dip	Syrphidae				7
	A68	Dip	Syrphidae				1
	A82	Hym	Anthophoridae				1
	A83	Hym	Anthophoridae				1
	A85	Hym	Anthophoridae				2
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	7
	A92	Hym	Colletidae				2
	A95	Hym	Eumenidae				1
	A106	Hym	Formicidae				2
	A124	Lep	Lycaenidae	Lycaeninae			1
3	A54	Dip	Muscidae				3
	A65	Dip	Syrphidae				3
	A114	Hym	Megachilidae				3
4	A12	Col	Coccinellidae				1
	A13	Col	Elateridae	Cardiophorinae	*Cardiophorus*		1
	A23	Col	Scarabaeidae	Cetoniinae			1
	A27	Col	Scarabaeidae	Cetoniinae			4

Study site	Animal code	Order	Family	Subfamily	Genus	Species	Indivi-duals
	A28	Col	Scarabaeidae	Scarabaeinae			1
	A34	Dip	Bombyliidae				1
	A44	Dip	Conopidae				1
	A47	Dip	Dolichopodidae				1
	A51	Dip	Muscidae				1
	A53	Dip	Muscidae				2
	A54	Dip	Muscidae				29
	A55	Dip	Muscidae				2
	A58	Dip	Pipunculidae				1
	A59	Dip	Sarcophagidae				1
	A65	Dip	Syrphidae				1
	A68	Dip	Syrphidae				1
	A80	Hym	Anthophoridae				1
	A82	Hym	Anthophoridae				2
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	34
	A87	Hym	Apidae				3
	A88	Hym	Colletidae				1
	A89	Hym	Colletidae				1
	A90	Hym	Colletidae				1
	A91	Hym	Colletidae				2
	A92	Hym	Colletidae				2
	A96	Hym	Eumenidae				1
	A107	Hym	Halictidae				1
	A109	Hym	Halictidae				3
	A114	Hym	Megachilidae				7
	A126	Lep	Noctuidae				2
5	A3	Col	Cerambycidae	Cerambycinae			2
	A10	Col	Coccinellidae				1
	A23	Col	Scarabaeidae	Cetoniinae			2
	A31	Col					1
	A39	Dip	Calliphoridae				3
	A41	Dip	Calliphoridae				1
	A44	Dip	Conopidae				6
	A48	Dip	Muscidae				2
	A49	Dip	Muscidae				1
	A50	Dip	Muscidae				4
	A51	Dip	Muscidae				4
	A52	Dip	Muscidae				2
	A53	Dip	Muscidae				3
	A54	Dip	Muscidae				24
	A55	Dip	Muscidae				4
	A56	Dip	Muscidae				1
	A62	Dip	Syrphidae				1
	A63	Dip	Syrphidae				1
	A64	Dip	Syrphidae				1
	A65	Dip	Syrphidae				2
	A66	Dip	Syrphidae				2
	A67	Dip	Syrphidae				1
	A68	Dip	Syrphidae				2
	A71	Dip	Tephritidae	Dacinae	*Didacus*		1
	A72	Dip	Tephritidae				1

Study site	Animal code	Order	Family	Subfamily	Genus	Species	Indivi-duals
	A76	Dip					1
	A78	Hym	Andrenidae				1
	A79	Hym	Anthophoridae	Xylocopinae	*Allodapula*	*variegata*	1
	A81	Hym	Anthophoridae				1
	A84	Hym	Anthophoridae				6
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	24
	A88	Hym	Colletidae				2
	A89	Hym	Colletidae				2
	A90	Hym	Colletidae				1
	A91	Hym	Colletidae				9
	A92	Hym	Colletidae				2
	A96	Hym	Eumenidae				2
	A101	Hym	Eumenidae				1
	A106	Hym	Formicidae				12
	A107	Hym	Halictidae				2
	A110	Hym	Ichneumonidae				1
	A114	Hym	Megachilidae				3
	A115	Hym	Pompilidae				1
	A118	Hym	Vespidae	Polistinae	*Polistes*	*fastidiotus*	1
	A120	Hym					1
6	A6	Col	Cerambycidae				1
	A9	Col	Chrysomelidae				5
	A13	Col	Elateridae	Cardiophorinae	*Cardiophorus*		2
	A14	Col	Lycidae	Lycinae	*Lycus*		1
	A21	Col	Scarabaeidae	Cetoniinae			2
	A23	Col	Scarabaeidae	Cetoniinae			1
	A24	Col	Scarabaeidae	Cetoniinae			1
	A30	Col					34
	A34	Dip	Bombyliidae				1
	A39	Dip	Calliphoridae				1
	A40	Dip	Calliphoridae				1
	A43	Dip	Conopidae				1
	A54	Dip	Muscidae				1
	A55	Dip	Muscidae				3
	A56	Dip	Muscidae				1
	A65	Dip	Syrphidae				1
	A68	Dip	Syrphidae				8
	A70	Dip	Tachinidae				3
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	12
	A92	Hym	Colletidae				2
	A106	Hym	Formicidae				14
	A126	Lep	Noctuidae				1
	A136	Lep	Pieridae	Pierinae	*Colotis*	*auxo*	1
	A138	Lep	Pieridae	Pierinae	*Dixeia*	*charina charina*	1
7	A20	Col	Scarabaeidae	Cetoniinae			1
	A23	Col	Scarabaeidae	Cetoniinae			1
	A34	Dip	Bombyliidae				1
	A37	Dip	Bombyliidae				2
	A44	Dip	Conopidae				2
	A45	Dip	Conopidae				1

Study site	Animal code	Order	Family	Subfamily	Genus	Species	Indivi-duals
	A52	Dip	Muscidae				2
	A60	Dip	Sciomyzidae				1
	A64	Dip	Syrphidae				1
	A67	Dip	Syrphidae				3
	A75	Dip					1
	A80	Hym	Anthophoridae				1
	A82	Hym	Anthophoridae				1
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	1
	A91	Hym	Colletidae				2
	A125	Lep	Lycidae				1
	A131	Lep	Papilionidae	Papilioninae	*Papilio*	*nireus lyaeus*	1
	A132	Lep	Pieridae	Coliadinae	*Catopsilia*	*florella*	2
	A136	Lep	Pieridae	Pierinae	*Colotis*	*auxo*	1
8	A3	Col	Cerambycidae	Cerambycinae			1
	A9	Col	Chrysomelidae				2
	A21	Col	Scarabaeidae	Cetoniinae			13
	A23	Col	Scarabaeidae	Cetoniinae			12
	A32	Dip	Acroceridae	Acrocerinae	*Psilodera*	*fasciata*	1
	A33	Dip	Acroceridae	Acrocerinae	*Psilodera*		1
	A58	Dip	Pipunculidae				1
	A68	Dip	Syrphidae				1
	A70	Dip	Tachinidae				3
	A82	Hym	Anthophoridae				1
	A83	Hym	Anthophoridae				2
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	3
	A87	Hym	Apidae				1
	A91	Hym	Colletidae				1
	A102	Hym	Formicidae				2
	A111	Hym	Masaridae				1
	A122	Lep	Hesperiidae	Coeliadinae	*Coeliades*	*keithloa keithloa*	1
	A133	Lep	Pieridae	Pierinae	*Belenois*	*creona severina*	1
	A134	Lep	Pieridae	Pierinae	*Belenois*	*gidica abyssinica*	3
	A136	Lep	Pieridae	Pierinae	*Colotis*	*auxo*	1
	A139	Lep					1
9	A9	Col	Chrysomelidae				2
	A13	Col	Elateridae	Cardiophorinae	*Cardiophorus*		5
	A18	Col	Scarabaeidae	Cetoniinae			1
	A22	Col	Scarabaeidae	Cetoniinae			3
	A23	Col	Scarabaeidae	Cetoniinae			4
	A25	Col	Scarabaeidae	Cetoniinae			1
	A41	Dip	Calliphoridae				1
	A53	Dip	Muscidae				1
	A79	Hym	Anthophoridae	Xylocopinae	*Allodapula*	*variegata*	1
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	1
	A88	Hym	Colletidae				1
	A92	Hym	Colletidae				1
	A97	Hym	Eumenidae				1
	A104	Hym	Formicidae				1
	A106	Hym	Formicidae				4
	A109	Hym	Halictidae				3

Study site	Animal code	Order	Family	Subfamily	Genus	Species	Indivi-duals
	A119	Hym	Vespidae				3
	A121	Hym					1
	A134	Lep	Pieridae	Pierinae	*Belenois*	*gidica abyssinica*	2
	A136	Lep	Pieridae	Pierinae	*Colotis*	*auxo*	1
10	A4	Col	Cerambycidae	Cerambycinae			1
	A9	Col	Chrysomelidae				7
	A19	Col	Scarabaeidae	Cetoniinae			1
	A23	Col	Scarabaeidae	Cetoniinae			1
	A56	Dip	Muscidae				1
	A79	Hym	Anthophoridae	Xylocopinae	*Allodapula*	*variegata*	3
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	3
	A92	Hym	Colletidae				1
	A104	Hym	Formicidae				6
	A106	Hym	Formicidae				15
11	A7	Col	Chrysomelidae	Cryptocephalinae	*Cryptocephalus*	*decemnotatus*	1
	A9	Col	Chrysomelidae				3
	A21	Col	Scarabaeidae	Cetoniinae			3
	A23	Col	Scarabaeidae	Cetoniinae			1
	A25	Col	Scarabaeidae	Cetoniinae			7
	A27	Col	Scarabaeidae	Cetoniinae			1
	A47	Dip	Dolichopodidae				1
	A55	Dip	Muscidae				1
	A70	Dip	Tachinidae				1
	A79	Hym	Anthophoridae	Xylocopinae	*Allodapula*	*variegata*	2
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	1
	A94	Hym	Eumenidae	Eumeninae	*Delta*		2
	A119	Hym	Vespidae				1
	A126	Lep	Noctuidae				1
	A130	Lep	Papilionidae	Papilioninae	*Graphium*	*leonidae leonidas*	1
	A134	Lep	Pieridae	Pierinae	*Belenois*	*gidica abyssinica*	1
	A135	Lep	Pieridae	Pierinae	*Belenois*	*zochalia zochalia*	2
12	A8	Col	Chrysomelidae				1
	A9	Col	Chrysomelidae				1
	A13	Col	Elateridae	Cardiophorinae	*Cardiophorus*		8
	A22	Col	Scarabaeidae	Cetoniinae			1
	A23	Col	Scarabaeidae	Cetoniinae			1
	A30	Col					1
	A51	Dip	Muscidae				1
	A78	Hym	Andrenidae				1
	A98	Hym	Eumenidae				1
	A103	Hym	Formicidae				16
	A104	Hym	Formicidae				31
	A105	Hym	Formicidae				26
	A106	Hym	Formicidae				2
	A107	Hym	Halictidae				1
	A112	Hym	Megachilidae				1
	A134	Lep	Pieridae	Pierinae	*Belenois*	*gidica abyssinica*	1
13	A9	Col	Chrysomelidae				1

Study site	Animal code	Order	Family	Subfamily	Genus	Species	Individuals
	A21	Col	Scarabaeidae	Cetoniinae			13
	A23	Col	Scarabaeidae	Cetoniinae			7
	A34	Dip	Bombyliidae				1
	A35	Dip	Bombyliidae				1
	A36	Dip	Bombyliidae				1
	A44	Dip	Conopidae				4
	A53	Dip	Muscidae				1
	A54	Dip	Muscidae				7
	A56	Dip	Muscidae				1
	A67	Dip	Syrphidae				2
	A70	Dip	Tachinidae				12
	A73	Dip	Tephritidae				1
	A79	Hym	Anthophoridae	Xylocopinae	*Allodapula*	*variegata*	14
	A80	Hym	Anthophoridae				2
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	32
	A87	Hym	Apidae				1
	A89	Hym	Colletidae				1
	A91	Hym	Colletidae				2
	A92	Hym	Colletidae				2
	A96	Hym	Eumenidae				1
	A97	Hym	Eumenidae				1
	A100	Hym	Eumenidae				1
	A106	Hym	Formicidae				9
	A107	Hym	Halictidae				1
	A108	Hym	Halictidae				1
	A109	Hym	Halictidae				1
	A112	Hym	Megachilidae				2
	A113	Hym	Megachilidae				1
	A117	Hym	Sphecidae				1
	A119	Hym	Vespidae				2
14	A5	Col	Cerambycidae	Cerambycinae			1
	A23	Col	Scarabaeidae	Cetoniinae			5
	A27	Col	Scarabaeidae	Cetoniinae			1
	A44	Dip	Conopidae				1
	A47	Dip	Dolichopodidae				2
	A53	Dip	Muscidae				1
	A54	Dip	Muscidae				9
	A56	Dip	Muscidae				2
	A57	Dip	Phoridae				2
	A63	Dip	Syrphidae				3
	A67	Dip	Syrphidae				1
	A79	Hym	Anthophoridae	Xylocopinae	*Allodapula*	*variegata*	2
	A82	Hym	Anthophoridae				2
	A85	Hym	Anthophoridae				1
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	28
	A87	Hym	Apidae				1
	A89	Hym	Colletidae				1
	A91	Hym	Colletidae				3
	A108	Hym	Halictidae				1
	A128	Lep	Nymphalidae	Nymphalinae	*Hypolimnas*	*anthedon wahlbergi*	1
	A134	Lep	Pieridae	Pierinae	*Belenois*	*gidica abyssinica*	1

Study site	Animal code	Order	Family	Subfamily	Genus	Species	Indivi-duals
15	A1	Col	Cerambycidae	Cerambycinae			1
	A3	Col	Cerambycidae	Cerambycinae			5
	A4	Col	Cerambycidae	Cerambycinae			1
	A9	Col	Chrysomelidae				2
	A11	Col	Coccinellidae				1
	A14	Col	Lycidae	Lycinae	*Lycus*		1
	A17	Col	Scarabaeidae	Cetoniinae			1
	A19	Col	Scarabaeidae	Cetoniinae			3
	A21	Col	Scarabaeidae	Cetoniinae			3
	A23	Col	Scarabaeidae	Cetoniinae			5
	A26	Col	Scarabaeidae	Cetoniinae			1
	A29	Col					1
	A30	Col					2
	A31	Col					2
	A39	Dip	Calliphoridae				1
	A42	Dip	Conopidae				2
	A43	Dip	Conopidae				2
	A44	Dip	Conopidae				2
	A46	Dip	Dolichopodidae				1
	A47	Dip	Dolichopodidae				1
	A50	Dip	Muscidae				1
	A51	Dip	Muscidae				5
	A52	Dip	Muscidae				1
	A53	Dip	Muscidae				7
	A54	Dip	Muscidae				39
	A55	Dip	Muscidae				16
	A56	Dip	Muscidae				1
	A57	Dip	Phoridae				1
	A61	Dip	Syrphidae	Eristalinae	*Eristalinus*	*taeniops*	1
	A65	Dip	Syrphidae				7
	A68	Dip	Syrphidae				3
	A70	Dip	Tachinidae				2
	A74	Dip	Tipulidae				1
	A78	Hym	Andrenidae				1
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	24
	A88	Hym	Colletidae				1
	A90	Hym	Colletidae				1
	A91	Hym	Colletidae				5
	A92	Hym	Colletidae				2
	A116	Hym	Sphecidae	Sphecinae	*Prionyx*		1
	A117	Hym	Sphecidae				1
	A119	Hym	Vespidae				1
	A139	Lep					1
16	A15	Col	Meloidae				1
	A23	Col	Scarabaeidae	Cetoniinae			3
	A24	Col	Scarabaeidae	Cetoniinae			4
	A27	Col	Scarabaeidae	Cetoniinae			29
	A29	Col					1
	A30	Col					17
	A31	Col					1

Study site	Animal code	Order	Family	Subfamily	Genus	Species	Individuals
	A52	Dip	Muscidae				1
	A53	Dip	Muscidae				1
	A54	Dip	Muscidae				5
	A55	Dip	Muscidae				1
	A68	Dip	Syrphidae				1
	A70	Dip	Tachinidae				4
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	52
	A121	Hym					2
17	A2	Col	Cerambycidae	Cerambycinae			1
	A9	Col	Chrysomelidae				1
	A11	Col	Coccinellidae				1
	A23	Col	Scarabaeidae	Cetoniinae			2
	A30	Col					1
	A51	Dip	Muscidae				1
	A52	Dip	Muscidae				1
	A54	Dip	Muscidae				1
	A66	Dip	Syrphidae				3
	A69	Dip	Syrphidae				1
	A82	Hym	Anthophoridae				1
	A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	86
	A91	Hym	Colletidae				5
	A99	Hym	Eumenidae				1
	A107	Hym	Halictidae				1
	A111	Hym	Masaridae				1
	A123	Lep	Hesperiidae				1
	A125	Lep	Lycidae				1
	A129	Lep	Nymphalidae	Nymphalinae	*Vanessa*	*cardui*	1
	A139	Lep					1

Appendix chapter 3

Table S3.1 Mean trait values and abundance of 131 pollinator species (species + morphospecies) in 17 plant–pollinator communities. Pollinators were indentified to the lowest taxonomic resolution possible and afterwards sorted into morphospecies (animal code). Pollinator identification followed Picker et al. (2004), Woodhall (2005) and Scholtz and Holm (2008). Methods of measurements of pollinator traits are given in Stang et al. (2006). The species list is ordered alphabetically by order and family (Col = Coleoptera; Dip = Diptera; Hym = Hymenoptera; Lep = Lepidoptera; NaN = cases in which measurements of specific pollinator traits were not feasible (e.g. because species were damaged; M = number of pollinator individuals used for measurements; R = number of represented individuals of the respective species among the 17 plant–pollinator communities). Animal codes refer to the codes used in a previously published study on the network structure of the plant–pollinator communities (Grass et al. 2013).

Code	Order	Family	Subfamily	Genus	Species	Proboscis length [mm]	Proboscis diameter [mm]	Body length [mm]	M	R
A1	Col	Cerambycidae	Cerambycinae			1.3	0.1	17.4	1	1
A2	Col	Cerambycidae	Cerambycinae			0.5	0.2	46.1	1	1
A3	Col	Cerambycidae	Cerambycinae			0.3	0.1	13.5	8	8
A4	Col	Cerambycidae	Cerambycinae			0.5	0.1	24.3	2	2
A5	Col	Cerambycidae	Cerambycinae			0.4	0.1	33.2	1	1
A6	Col	Cerambycidae				0.3	0.2	21.8	1	1
A7	Col	Chrysomelidae	Cryptocephalinae	*Cryptocephalus*	*decemnotatus*	0.3	0.1	9.4	1	1
A8	Col	Chrysomelidae				0.8	0.2	13.2	2	2
A9	Col	Chrysomelidae				0.5	0.1	8.0	11	30
A10	Col	Coccinellidae				5.3	0.4	15.2	1	1
A11	Col	Coccinellidae				0.4	0.1	10.4	2	2
A12	Col	Coccinellidae				0.7	0.1	16.6	1	1
A13	Col	Elateridae	Cardiophorinae	*Cardiophorus*		0.3	0.1	10.5	8	16
A14	Col	Lycidae	Lycinae	*Lycus*		1.3	0.3	22.7	2	2
A15	Col	Meloidae				1.3	0.2	15.2	1	1
A16	Col	Scarabaeidae	Cetoniinae			0.8	0.2	22.0	7	7
A17	Col	Scarabaeidae	Cetoniinae			0.6	0.1	27.0	1	1
A18	Col	Scarabaeidae	Cetoniinae			0.6	0.3	24.3	1	1
A19	Col	Scarabaeidae	Cetoniinae			0.4	0.2	20.7	4	4
A20	Col	Scarabaeidae	Cetoniinae			0.8	0.2	20.4	3	3
A21	Col	Scarabaeidae	Cetoniinae			0.4	0.1	15.9	8	42
A22	Col	Scarabaeidae	Cetoniinae			0.7	0.2	24.0	4	4
A23	Col	Scarabaeidae	Cetoniinae			0.5	0.1	19.6	7	53
A24	Col	Scarabaeidae	Cetoniinae			0.5	0.1	17.6	5	5
A25	Col	Scarabaeidae	Cetoniinae			0.5	0.1	15.6	7	8
A26	Col	Scarabaeidae	Cetoniinae			1.3	0.2	28.2	1	1
A27	Col	Scarabaeidae	Cetoniinae			0.5	0.1	12.8	8	37
A28	Col	Scarabaeidae	Scarabaeinae			0.4	0.2	10.8	1	1
A29	Col					0.3	0.1	14.9	2	2
A30	Col					1.1	0.2	15.3	8	55
A31	Col					0.5	0.2	9.7	5	5
A32	Dip	Acroceridae	Acrocerinae	*Psilodera*	*fasciata*	12.1	0.4	14.1	1	1
A33	Dip	Acroceridae	Acrocerinae	*Psilodera*		17.4	1.1	22.1	1	1
A35	Dip	Bombyliidae				9.1	0.3	20.5	1	1
A36	Dip	Bombyliidae				7.1	1.0	29.8	1	1

Code	Order	Family	Subfamily	Genus	Species	Proboscis length [mm]	Proboscis diameter [mm]	Body length [mm]	M	R
A37	Dip	Bombyliidae				3.6	0.2	15.2	2	2
A38	Dip	Bombyliidae				2.2	0.3	17.2	1	1
A39	Dip	Calliphoridae				3.5	1.0	17.5	6	5
A40	Dip	Calliphoridae				2.2	0.3	10.0	1	1
A41	Dip	Calliphoridae				2.8	0.9	13.2	2	2
A42	Dip	Conopidae				1.0	0.5	13.0	8	8
A43	Dip	Conopidae				2.5	0.7	15.2	3	3
A44	Dip	Conopidae				1.4	0.3	7.7	7	17
A45	Dip	Conopidae				1.6	0.4	12.7	1	1
A46	Dip	Dolichopodidae				4.3	0.2	13.2	1	1
A47	Dip	Dolichopodidae				4.5	0.1	9.3	5	5
A48	Dip	Muscidae				2.5	0.5	16.7	4	3
A49	Dip	Muscidae				1.7	0.3	12.6	1	1
A50	Dip	Muscidae				2.4	0.3	13.3	5	6
A51	Dip	Muscidae				1.8	0.4	10.5	8	12
A52	Dip	Muscidae				3.3	0.1	8.4	8	8
A54	Dip	Muscidae				2.0	0.6	14.6	8	127
A55	Dip	Muscidae				2.5	0.5	13.0	8	28
A56	Dip	Muscidae				2.5	0.6	13.7	7	16
A57	Dip	Phoridae				1.7	0.4	8.9	3	3
A58	Dip	Pipunculidae				1.0	0.5	13.4	2	3
A59	Dip	Sarcophagidae				0.9	1.1	16.8	1	1
A60	Dip	Sciomyzidae				1.1	0.6	17.1	1	1
A61	Dip	Syrphidae	Eristalinae	*Eristalinus*	*taeniops*	2.1	1.0	29.6	1	1
A62	Dip	Syrphidae				3.3	1.1	18.8	1	1
A63	Dip	Syrphidae				6.0	0.4	21.1	4	5
A64	Dip	Syrphidae				2.2	1.0	15.2	4	2
A65	Dip	Syrphidae				1.8	0.8	16.4	8	22
A66	Dip	Syrphidae				4.6	0.5	25.4	5	5
A67	Dip	Syrphidae				1.6	0.5	15.2	8	13
A68	Dip	Syrphidae				1.2	0.9	13.8	8	23
A69	Dip	Syrphidae				2.5	1.1	17.6	1	1
A70	Dip	Tachinidae				3.7	0.6	17.4	8	25
A71	Dip	Tephritidae	Dacinae	*Didacus*		2.0	1.2	13.5	1	1
A73	Dip	Tephritidae				1.4	0.5	10.6	1	1
A74	Dip	Tipulidae				4.3	0.1	53.0	1	1
A75	Dip					10.7	0.9	10.4	1	1
A77	Dip					0.6	0.2	10.9	2	1
A79	Hym	Anthophoridae	Xylocopinae	*Allodapula*	*variegata*	3.9	0.1	11.1	8	37
A80	Hym	Anthophoridae				4.3	0.1	13.1	8	8
A81	Hym	Anthophoridae				6.1	0.6	22.5	1	1
A82	Hym	Anthophoridae				4.6	0.1	10.5	8	9
A83	Hym	Anthophoridae				10.9	0.2	19.8	3	3
A84	Hym	Anthophoridae				4.8	0.2	12.3	6	6
A85	Hym	Anthophoridae				5.2	0.3	10.5	4	4
A86	Hym	Apidae	Apinae	*Apis*	*mellifera*	4.6	0.7	21.1	8	367
A87	Hym	Apidae				5.9	0.2	15.7	6	6
A88	Hym	Colletidae				6.7	0.2	11.4	5	5
A89	Hym	Colletidae				1.9	0.1	10.3	9	4
A91	Hym	Colletidae				3.5	0.1	13.3	9	31

Code	Order	Family	Subfamily	Genus	Species	Proboscis length [mm]	Proboscis diameter [mm]	Body length [mm]	M	R
A92	Hym	Colletidae				2.7	0.3	10.6	8	24
A93	Hym	Eumenidae	Eumeninae	*Delta*	*emarginatum*	2.2	1.0	36.8	1	1
A94	Hym	Eumenidae	Eumeninae	*Delta*		5.3	0.2	29.1	3	3
A95	Hym	Eumenidae				1.0	NaN	41.6	1	1
A96	Hym	Eumenidae				3.3	0.1	16.2	5	5
A97	Hym	Eumenidae				2.6	0.3	20.3	2	2
A98	Hym	Eumenidae				1.8	0.1	15.1	1	1
A99	Hym	Eumenidae				NaN	NaN	17.9	1	1
A100	Hym	Eumenidae				2.1	0.4	13.4	1	1
A101	Hym	Eumenidae				2.1	0.9	18.8	1	1
A102	Hym	Formicidae				NaN	NaN	20.7	2	2
A103	Hym	Formicidae				1.2	0.4	13.2	8	16
A104	Hym	Formicidae				0.8	0.1	10.1	8	38
A105	Hym	Formicidae				1.1	0.2	12.8	7	26
A106	Hym	Formicidae				1.2	0.5	17.4	8	60
A107	Hym	Halictidae				5.7	0.3	12.2	6	8
A108	Hym	Halictidae				2.0	0.1	8.5	2	2
A109	Hym	Halictidae				3.1	0.1	7.6	7	18
A110	Hym	Ichneumonidae				0.3	0.1	10.5	1	1
A111	Hym	Masaridae				6.4	0.6	15.0	2	2
A112	Hym	Megachilidae				9.8	0.4	27.8	3	3
A113	Hym	Megachilidae				7.0	0.3	23.5	1	1
A114	Hym	Megachilidae				3.8	0.1	7.7	7	13
A115	Hym	Pompilidae				2.4	0.4	16.7	1	1
A116	Hym	Sphecidae	Sphecinae	*Prionyx*		2.5	NaN	29.6	1	1
A117	Hym	Sphecidae				2.2	0.3	16.5	2	2
A118	Hym	Vespidae	Polistinae	*Polistes*	*fastidiotus*	1.5	0.8	31.0	1	1
A119	Hym	Vespidae				2.6	0.1	10.2	8	8
A120	Hym					1.3	0.1	6.8	1	1
A121	Hym					0.7	NaN	9.1	4	4
A122	Lep	Hesperiidae	Coeliadinae	*Coeliades*	*keithloa keithloa*	22.0	0.4	36.2	1	1
A123	Lep	Hesperiidae				18.5	0.2	19.6	1	1
A125	Lep	Lycaenidae				7.6	0.1	12.2	2	2
A127	Lep	Nymphalidae	Heliconiinae	*Hyalites*	*esebria esebria*	17.5	0.2	24.7	1	1
A128	Lep	Nymphalidae	Nymphalinae	*Hypolimnas*	*anthedon wahlbergi*	17.0	0.3	30.6	1	1
A129	Lep	Nymphalidae	Nymphalinae	*Vanessa*	*cardui*	26.0	0.5	34.3	1	1
A130	Lep	Papilionidae	Papilioninae	*Graphium*	*leonidae leonidas*	16.5	0.7	35.2	1	1
A131	Lep	Papilionidae	Papilioninae	*Papilio*	*nireus lyaeus*	35.3	0.6	39.0	1	1
A132	Lep	Pieridae	Coliadinae	*Catopsilia*	*florella*	19.9	0.3	27.0	4	3
A133	Lep	Pieridae	Pierinae	*Belenois*	*creona severina*	16.1	0.5	26.1	1	1
A134	Lep	Pieridae	Pierinae	*Belenois*	*gidica abyssinica*	18.2	0.4	24.7	12	12
A135	Lep	Pieridae	Pierinae	*Belenois*	*zochalia zochalia*	19.5	0.5	23.4	3	3
A136	Lep	Pieridae	Pierinae	*Colotis*	*auxo*	21.3	0.5	19.3	3	4
A137	Lep	Pieridae	Pierinae	*Colotis*	*ione*	21.5	0.4	18.1	1	1
A138	Lep	Pieridae	Pierinae	*Dixeia*	*charina charina*	16.7	0.3	20.8	6	6
A139	Lep					4.1	0.2	12.0	7	5

Table S3.2 Effects of natural habitat loss and relative exotic abundance on species richness (log10-transformed) of pollinators. Effects were corrected for plant origin (native vs. exotic) and the relative floral abundance of a focal plant species on the total floral abundance of all flowering plant species in a given study site (ln-transformed). Predictors were standardized to zero mean and unit variance to ease the comparison of effect sizes.

Source of variation	Estimate	*Z*	*P*
Relative abundance	0.20	3.1	0.0022
Plant origin	-0.47	-3.5	< 0.001
Natural habitat loss	0.10	0.84	0.40
Relative exotic abundance	0.18	1.3	0.19
Natural habitat loss × Relative exotic abundance	0.033	0.31	0.76

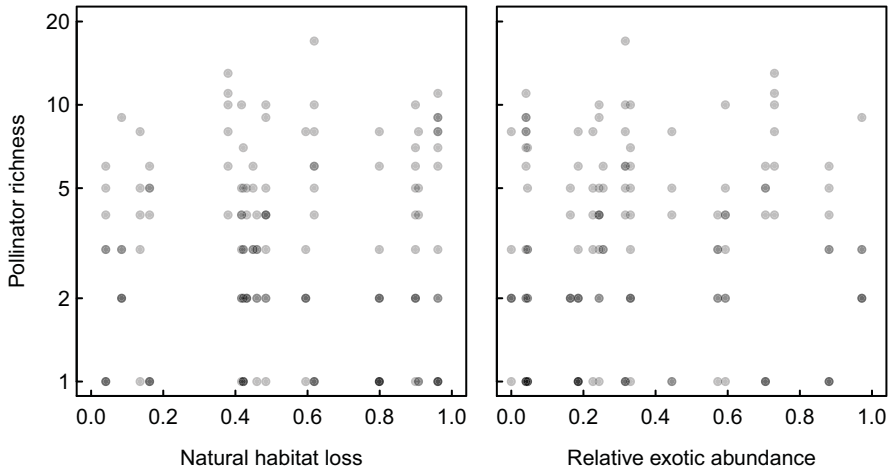

Fig. S3.1 Species richness of pollinators on plant species along gradients of increasing natural habitat loss and relative exotic abundance in a subtropical landscape (observed on 131 plant species across 17 plant–pollinator communities). Data points are semitransparent so that multiple points at the same location appear darker. Note log10-transformed axis for pollinator richness.

Assessing changes in community composition of plant species with natural habitat loss and relative exotic abundance

Changes in pollinator FD with natural habitat loss and relative exotic abundance might have been driven by changes in the composition of the sampled plant communities. To investigate changes in community composition of plant species, we first constructed a plant species × study site matrix based on Bray-Curtis distances of mean flower abundances of plant species. We then used non-parametric permutational MANOVA (function 'adonis' in R package vegan; Oksanen et al. 2012) to partition variation in plant species composition with natural habitat loss and relative exotic abundance, and assessed statistical significance by permuting the raw data (999 permutations). Variation in plant species composition was not explained by increases in natural habitat loss across study sites (R^2 = 0.084, $F_{1,15}$ = 1.4, P = 0.12), yet differed with relative exotic abundance (R^2 = 0.098, $F_{1,15}$ = 1.6, P = 0.029). Using a Hellinger-transformed species × study site matrix to account for the large number of zero entries (Legendre and Gallagher 2001) yielded qualitatively similar results (natural habitat loss: R^2 = 0.095, $F_{1,15}$ = 1.6, P = 0.089; relative exotic abundance: R^2 = 0.10, $F_{1,15}$ = 1.7, P = 0.040). These results indicated that the detected loss in pollinator FD with natural habitat loss was probably not attributable to changes in plant species composition across study sites. However, as may be expected, increasing relative exotic abundance resulted in changes in plant species composition, which may have affected the observed patterns in pollinator FD.

Accounting for differences in specific functional traits of plant species

To further disentangle the relative contributions of study site characteristics and effects associated with plant species identities, we aimed at incorporating information of plant species traits in our models. We used plant traits, which we assumed to be directly linked to our investigated pollinator traits. These traits included depth and width of the nectar holder and size of the alighting place of a plant species (corresponding to proboscis length, proboscis diameter and body length, respectively; Stang et al. 2006). Depending on abundance, traits were measured on up to ten inflorescences per plant species. Measurements were conducted to the nearest 0.1 mm, following the methods outlaid in Stang et al. (2006). We then compared results from linear-mixed effects models on changes in pollinator FD with natural habitat loss and relative exotic abundance (using the same model structures as described in the main text) before and after including these plant

traits as additional covariates. Including the plant traits into our models did not quantitatively or qualitatively alter previous results or the effects sizes of natural habitat loss and relative exotic abundance and their statistical significance (Table S3.3). Thus, in contrast to natural habitat loss and relative exotic abundance across study sites, functional traits of a given plant species did not substantially drive changes in pollinator FD.

Table S3.3 Plant traits that were included as additional covariates in statistical models to predict changes in pollinator FD with natural habitat loss and relative exotic abundance. Given are effect sizes (i.e. estimates) and *Z*-values (in brackets) of the effects of natural habitat loss and relative exotic abundance before (see manuscript) and after including additional covariates into linear mixed-effects models. Further shown are effect sizes and *Z*-values of additionally included covariates. Significant effects ($P < 0.050$) are indicated in bold. Note that there were no interactive effects between natural habitat loss and relative exotic abundance before or after including additional covariates.

Response	**Additional covariate(s)**			**Before inclusion**		**After inclusion**	
	Nectar holder depth	Nectar holder width	Alighting place	Natural habitat loss	Relative exotic abundance	Natural habitat loss	Relative exotic abundance
Multivariate FD	-0.013 [-0.35]	-0.014 [-0.34]	**0.089 [2.3*]**	**- 0.14 [-3.1**]**	**-0.12 [-2.2*]**	**-0.14 [-3.1**]**	**-0.13 [-2.4*]**
FD in proboscis length	0.037 [1.4]			**-0.088 [-2.6*]**	-0.049 [-1.2]	**-0.083 [-2.4*]**	-0.046 [-1.2]
FD in proboscis diameter		-0.0061 [-0.24]		-0.057 [-1.8]	-0.053 [-1.4]	-0.058 [-1.8]	-0.054 [-1.4]
FD in body length			0.032 [1.48]	**-0.063 [-2.4*]**	**-0.065 [-2.1*]**	**-0.061 [-2.3*]**	**-0.068 [-2.2*]**

** $P < 0.010$; * $P < 0.050$

Accounting for phylogenetic relatedness of plant species

Instead of using specific functional traits, information on the overall phylogenetic relatedness among the plant species within a local community may be more informative, particularly when it is unclear which traits drive pollinator assembly (Cavender-Bares et al. 2009). Phylogenetically closely related plant species may share pollinator assemblages due to phylogenetic trait conservatism, whereas phylogenetically distantly related species may attract divergent pollinator assemblages via functional complementarity (Rezende et al. 2007). Similarly, phylogenetically distantly related plant species may show divergent pollinator assemblages owing to different co-evolutionary history, whereas closely related plants may share pollinator assemblages (Ehrlich and Raven 1964). If the phylogenetic structure of plant communities changed non-randomly with increasing natural habitat loss or relative exotic abundance (e.g. only phylogenetically closely related plant species remained), incorporating information on phylogenetic relatedness into our models should reduce effect sizes of natural habitat loss or relative exotic abundance on pollinator FD.

We generated a phylogenetic supertree using the software Phylomatic (Webb and Donoghue 2005), with branch lengths equal one as a full molecular phylogeny of our plant species was unavailable. We then calculated patristic distances among the 53 plant species in our phylogeny. As some plant species were present in multiple study sites, we expanded this distance matrix to the dimension of our FD measures, resulting in a matrix of 131 × 131 entries. We then used principal coordinates of neighbor matrices analysis (PCNM) to derive orthogonal phylogenetic eigenvectors of this matrix (Borcard et al. 2004; Diniz-Filho et al. 2012). Phylogenetic eigenvectors give information on the phylogenetic structure of the plant community, i.e. the relatedness of species, at different taxonomic levels (Diniz-Filho et al. 2012). For each multivariate and univariate measure of pollinator FD, we used forward selection at $\alpha = 0.050$ to identify phylogenetic eigenvectors that were potentially important predictors of pollinator FD (function 'forward.sel' in R package packfor; Dray et al. 2011). Similar to the analysis on the effects of specific functional traits of plants (see above) we then compared effect sizes and significance of the effects of natural habitat loss and relative exotic abundance on pollinator FD before and after including the selected phylogenetic eigenvectors into our models.

Inclusion of phylogenetic eigenvectors did not affect our conclusions regarding the effect sizes of natural habitat loss and relative exotic abundance on multivariate FD (Table S3.4). However, after correcting for phylogenetic relatedness among plant species, the

effect of natural habitat loss on FD in proboscis length was not statistically significant anymore (Table S3.4). In contrast, effects on FD in proboscis diameter and FD in body length were unaffected (Table S3.4). Some variance of FD in proboscis length among study sites therefore may have been driven by phylogenetic relatedness of the investigated plant species. However, the overall negative effects of increasing natural habitat loss and relative exotic abundance on all other measures of FD remained quantitatively and qualitatively similar. Thus, even in the presence of shifts in the phylogenetic structure of plant species communities, natural habitat loss and exotic plants are likely the most important drivers of loss in pollinator FD.

Table S3.4 Effects of natural habitat loss and relative exotic abundance before and after correcting for effects of phylogenetic relatedness among plant species. Phylogenetic relatedness was measured at different taxonomic scales, using phylogenetic eigenvector analysis. Given are effect sizes (i.e. estimates) and *Z*-values (in square brackets) of the effects of natural habitat loss and relative exotic abundance and additionally included eigenvectors. Significant effects ($P < 0.050$) are indicated in bold. Identity codes for eigenvectors are given in round brackets. Note that there were no interactive effects between natural habitat loss and relative exotic abundance before or after additionally including phylogenetic eigenvectors.

Response	**Additional eigenvectors**					**Before inclusion**		**After inclusion**	
	Eigenvector	Eigenvector	Eigenvector	Eigenvector	Eigenvector	Natural habitat loss	Relative exotic abundance	Natural habitat loss	Relative exotic abundance
Multivariate FD	**-1.6 [-4.2***]** (PCNM 34)	**1.1 [2.8**]** (PCNM 7)	0.53 [1.4] (PCNM 8)			**- 0.14 [-3.1**]**	**-0.12 [-2.2*]**	**-0.11 [-2.7**]**	**-0.11 [-2.1*]**
FD in proboscis length	**-1.2 [-4.2***]** (PCNM 34)	**-0.88 [-3.2**]** (PCNM 29)				**-0.088 [-2.6*]**	-0.049 [-1.2]	-0.055 [-1.7]	-0.025 [-0.67]
FD in proboscis diameter	**0.85 [3.3**]** (PCNM 7)	0.42 [1.6] (PCNM 8)	-0.36 [-1.4] (PCNM 32)			-0.057 [-1.8]	-0.053 [-1.4]	-0.046 [-1.5]	-0.051 [-1.5]
FD in body length	**-0.92 [-4.6***]** (PCNM 34)	**-0.60 [-3.1**]** (PCNM 14)	0.38 [1.9] (PCNM 7)	**0.40 [2.0*]** (PCNM 8)	**0.56 [2.8**]** (PCNM 29)	**-0.063 [-2.4*]**	**-0.065 [-2.1*]**	**-0.060 [-2.6**]**	**-0.069 [-2.6**]**

*** $P < 0.0010$; ** $P < 0.010$; * $P < 0.050$

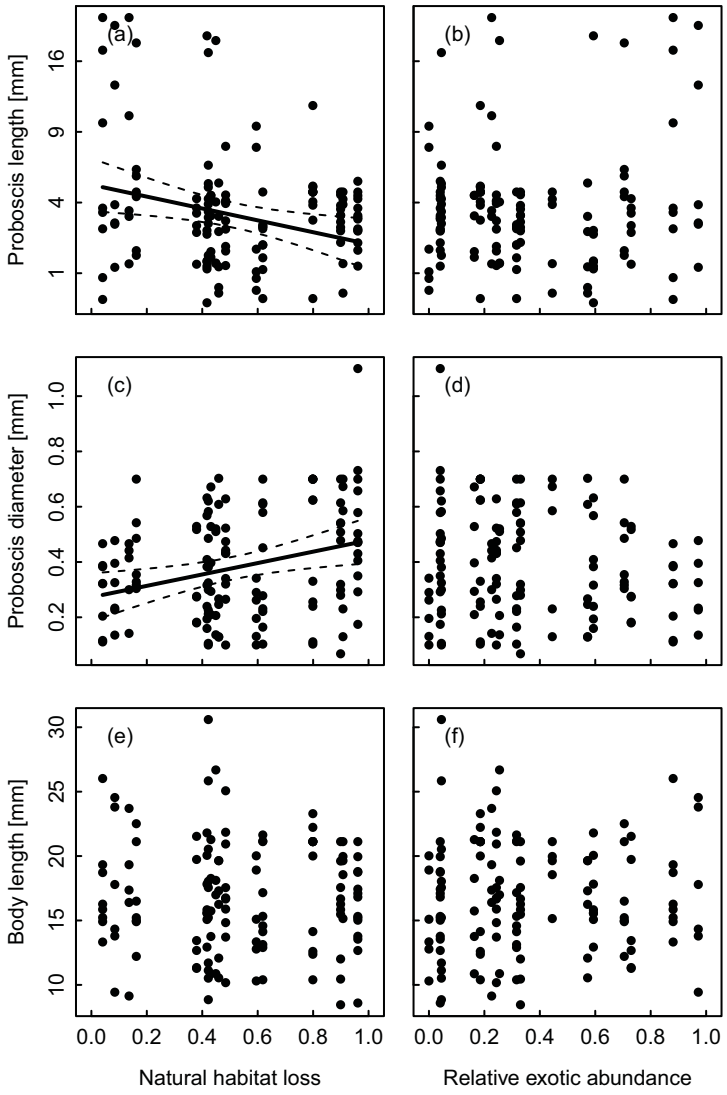

Fig S3.2 Weighted mean trait values of pollinators along increasing gradients of loss of natural habitat and relative exotic plant abundance in a subtropical heterogeneous landscape (observed on 131 plant species across 17 plant–pollinator communities). Natural habitat loss negatively affected weighted mean proboscis length of pollinators (panel a). Proboscis diameter increased with natural habitat loss but not with exotic abundance (c+d). Body length of pollinators was not related to natural habitat loss or relative exotic abundance per study site (e+f). Shown are effects of drivers from linear mixed-effects models (black line) and 95% confidence intervals (dashed lines). Effects are corrected for other covariates in models. Black points show the underlying raw data distribution. Note square-root axis for proboscis length.

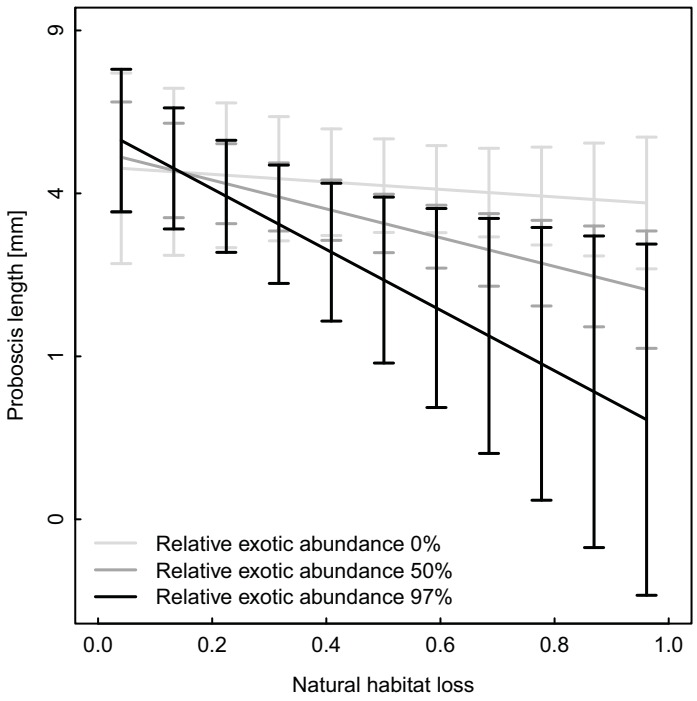

Fig S3.3 Changes in weighted mean proboscis length of pollinators with increasing natural habitat loss and relative abundance of exotic plant species across study site. The figure shows the negative synergistic effect between natural habitat loss and relative exotic abundance: decreases in proboscis length with increasing habitat loss are stronger in study sites with higher levels of plant invasion. Curves show the predicted effects (lines) of habitat loss on proboscis length under different degrees of invasion (relative exotic abundance) from a linear mixed-effects model. Arrows depict 95% confidence intervals. Note square-root axis for proboscis length.

Multivariate analysis

We used multivariate analysis to investigate which main pollinator groups drove the observed changes in weighted mean functional traits with increasing natural habitat loss and relative abundance of exotic plants. Here, we grouped pollinators according to their taxonomic families in order to decrease the complexity of the multivariate ordination and achieve homogeneity in the taxonomic resolution of different pollinator morphospecies. The abundance site × family matrix comprised 38 families or ~ 94% of all pollinator morphospecies (the remainder had not been identified to family level). We then applied a detrended correspondence analysis (DCA) using Bray-Curtis distances with Hellinger-transformed abundance data (Legendre and Gallagher 2001). Lengths of the first and second axis of the DCA ordination were 2.7 and 1.9, respectively. Afterwards we fitted natural habitat loss and relative exotic abundance as environmental variables on the two-dimensional ordination of the DCA ordination. To fit these environmental variables, we had to take into account that a given pollinator family could be present in multiple study sites with differing habitat conditions. We therefore calculated the mean habitat conditions under which a given family would occur in the field, by calculating a weighted mean of natural habitat loss and relative exotic abundance for each family, with family abundances across study sites as weights. We then used the 'ordisurf' function in R package 'vegan' (Oksanen et al. 2012) to fit smooth surfaces of the environmental variables. In contrast to fitting linear vectors, this method allows for non-linear relationships between environmental variables and ordination data, which in our case greatly improved the fit with the ordination. Both natural habitat loss ($R^2_{adj} = 0.61$, $P < 0.0010$) as well as relative exotic abundance ($R^2_{adj} = 0.71$, $P < 0.0010$) explained a high amount in variation in family composition. Finally, to visualize the different trait values of the plotted families, we calculated a weighted mean of each trait per family, which we standardized between 0 and 1. We then used these trait values to assign different color values to the family labels in the ordination (Fig S3.4).

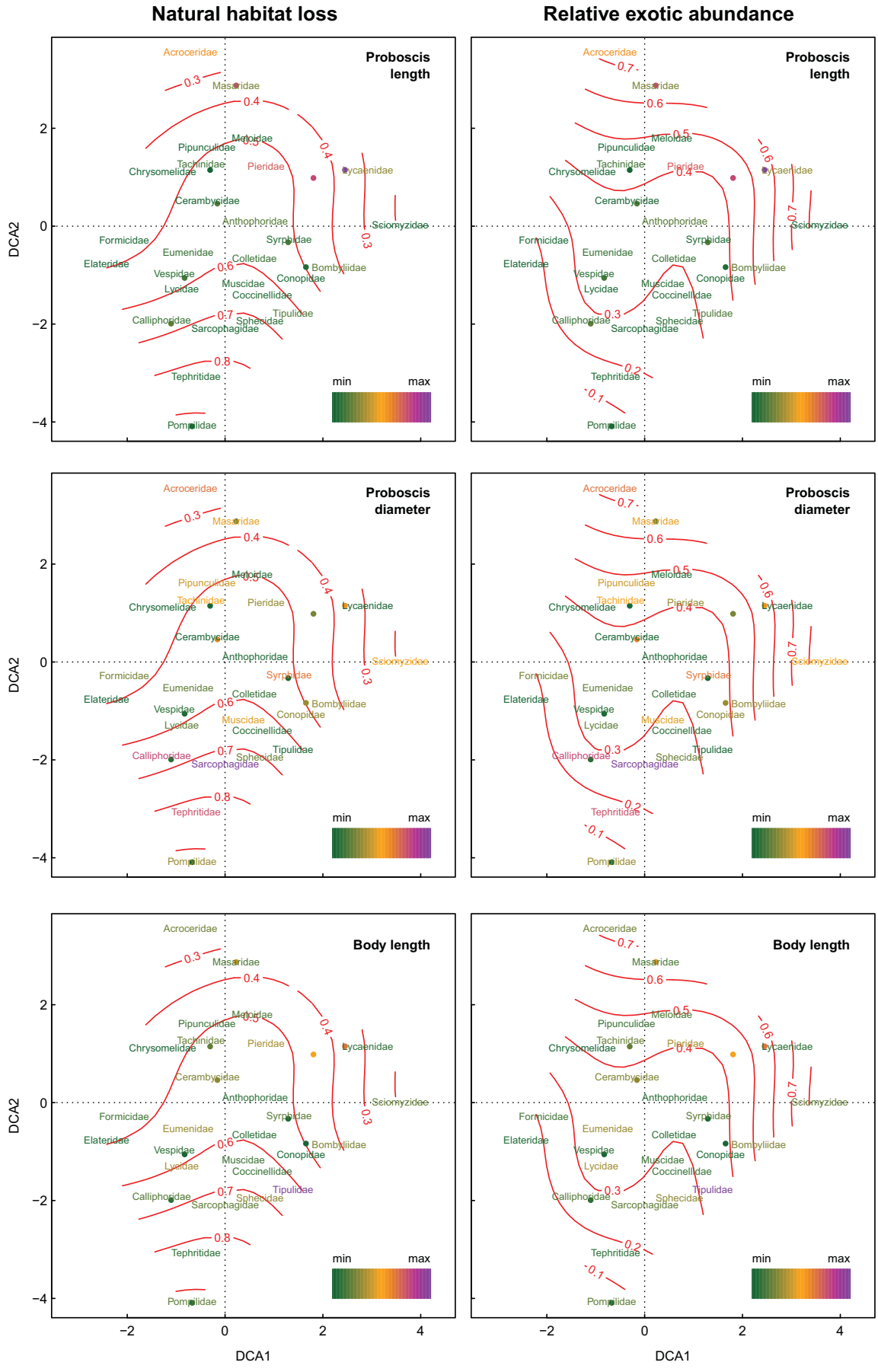
Natural habitat loss
Relative exotic abundance
Proboscis length
Proboscis diameter
Body length
min
max
DCA1
DCA2
Acroceridae
Asilidae
Meloidae
Pipunculidae
Tachinidae
Chrysomelidae
Pieridae
Lycaenidae
Cerambycidae
Anthophoridae
Sciomyzidae
Formicidae
Syrphidae
Eumenidae
Elateridae
Colletidae
Vespidae
Bombyliidae
Lycidae
Muscidae
Conopidae
Coccinellidae
Calliphoridae
Tipulidae
Sphecidae
Sarcophagidae
Tephritidae
Pompilidae

Fig S3.4 Ordinations of the detrended correspondence analysis (DCA) on pollinator family composition. Although based on one statistical analysis, six different ordination plots are shown to ease comparison of functional traits and effects of habitat loss and relative abundance of exotic plants. Families (n = 38) are shown in different colors according to their weighted mean functional traits, with trait values scaled between 0 (min) and 1 (max). Note that in cases of overlapping labels, filled circles are shown instead of family names. Red contours depict smooth surface fits of environmental variables (left column: natural habitat loss; right column: relative exotic abundance).

Appendix chapter 4

Table S4.1 Observed plant species during plant–frugivore observations. Species are sorted by scientific names.

Common name	Scientific name	Family	Plant origin
Tassel-berry	*Antidesma venosum*	Euphorbiaceae	native
White-pear	*Apodytes dimidiata*	Icacinaceae	native
Mitzeeri Sweetberry	*Bridelia micrantha*	Euphorbiaceae	native
White-stinkwood	*Celtis africana*	Celtidaceae	native
Camphor Tree	*Cinnamomum camphora*	Lauraceae	invasive
Forest Croton	*Croton sylvaticus*	Euphorbiaceae	native
Forest Coca-tree	*Erythroxylum pictum*	Erythroxylaceae	native
Common Wild Fig	*Ficus burkei*	Moraceae	native
Mountain Rock Fig	*Ficus glumosa*	Moraceae	native
Red-leaf Rock Fig	*Ficus ingens*	Moraceae	native
Cape Fig	*Ficus sur*	Moraceae	native
Lantana	*Lantana camara*	Verbenaceae	invasive
River Macaranga	*Macaranga capensis*	Euphorbiaceae	native
False-assegai	*Maesa lanceolata*	Myrsinaceae	native
Black Bird-berry	*Psychotria capensis*	Rubiaceae	native
Bugweed	*Solanum mauritianum*	Solanaceae	invasive
Waterberry	*Syzigium cordatum*	Myrtaceae	native
White-ironwood	*Vepris lanceolata*	Rutaceae	native

Table S4.2 Forest dependency, degree of frugivory and number of interactions of frugivore species observed feeding on fruit of plant species during plant–frugivore observations. Abbreviations of forest dependency: FS = forest specialist; FG = forest generalist; FV = forest visitor.

Common name	Scientific name	Forest dependency	Degree of frugivory	Interactions
African Dusky Flycatcher	*Muscicapa adusta*	FG	opportunistic	1
African Green-Pigeon	*Treron calvus*	FG	obligate	3
African Olive Pigeon	*Columba arquatrix*	FS	partial	9
African Stonechat	*Saxicola torquatus*	FV	opportunistic	2
Ashy Flycatcher	*Muscicapa caerulescens*	FG	opportunistic	60
Black-bellied Starling	*Lamprotornis corruscus*	FV	partial	17
Black-collared Barbet	*Lybius torquatus*	FG	obligate	55
Black-headed Oriole	*Oriolus larvatus*	FG	partial	24
Cape Glossy Starling	*Lamprotornis nitens*	FG	partial	32
Cape Weaver	*Ploceus capensis*	FV	opportunistic	1
Cape White-eye	*Zosterops pallidus*	FG	partial	532
Chorister Robin-Chat	*Cossypha dichroa*	FS	opportunistic	4
Dark-backed Weaver	*Ploceus bicolor*	FS	partial	15
Dark-capped Bulbul	*Pycnonotus barbatus*	FG	obligate	265
Forest Canary	*Serinus scotops*	FG	partial	1
Golden Weaver	*Ploceus xanthops*	FG	partial	1
Green Wood-Hoopoe	*Phoeniculus purpureus*	FG	opportunistic	9
Grey Sunbird	*Nectarinia veroxii*	FS	opportunistic	1
Knysna Turaco	*Tauraco corythaix*	FS	obligate	71
Kurrichane Thrush	*Turdus libonyanus*	FG	opportunistic	2
Marsh Warbler	*Acrocephalus palustris*	FV	opportunistic	1
Olive Sunbird	*Nectarinia olivacea*	FG	partial	4
Olive Thrush	*Turdus olivaceus*	FG	partial	48
Red-eyed Dove	*Streptopelia semitorquata*	FG	opportunistic	1
Red-fronted Tinkerbird	*Pogoniulus pusillus*	FG	obligate	2
Red-winged Starling	*Onychognathus morio*	FV	partial	18
Sombre Greenbul	*Andropadus importunus*	FS	obligate	22
Southern Black Flycatcher	*Melaenornis pammelaina*	FG	opportunistic	6
Southern Black Tit	*Parus niger*	FG	opportunistic	1
Southern Boubou	*Laniarius ferrugineus*	FG	opportunistic	1
Speckled Mousebird	*Colius striatus*	FG	obligate	152
Spectacled Weaver	*Ploceus ocularis*	FG	opportunistic	2
Spotted Flycatcher	*Muscicapa striata*	FG	opportunistic	1
Square-tailed Drongo	*Dicrurus ludwigii*	FS	opportunistic	4
Streaky-headed Seedeater	*Serinus gularis*	FV	partial	2
Tambourine Dove	*Turtur tympanistria*	FS	partial	18
Terrestrial Brownbul	*Phyllastrephus terrestris*	FS	opportunistic	9
Trumpeter Hornbill	*Bycanistes bucinator*	FG	obligate	28
Village Weaver	*Ploceus cucullatus*	FV	partial	3
White-bellied Sunbird	*Nectarinia talatala*	FG	opportunistic	1
Yellow-fronted Canary	*Serinus mozambicus*	FG	opportunistic	6
Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*	FS	obligate	11

Table S4.3 First 30 models of the model set used for model selection to predict guild-specific changes in frugivore visitation rates, with frugivore guilds divided by forest dependency (104 models in total). Inclusion of a predictor in a given model is indicated by a plus sign.

Inter-cept	FA	PO	FD	HL	IL	FD × PO	FD × HL	FD × IL	HL × IL	FD × HL × IL	k	logLik	AIC_c	Delta AIC_c	Model weight
+	+		+	+	+		+	+			13	-185.25	399.76	0.00	0.339
+	+	+	+	+	+		+	+			14	-184.18	400.15	0.39	0.279
+	+		+	+	+		+	+	+		14	-185.02	401.82	2.06	0.121
+	+	+	+	+	+		+	+	+		15	-183.95	402.27	2.51	0.097
+	+	+	+	+	+	+	+	+			16	-182.69	402.37	2.61	0.092
+	+	+	+	+	+	+	+	+	+		17	-182.46	404.59	4.83	0.030
+	+		+	+	+		+	+	+	+	16	-184.14	405.28	5.52	0.021
+	+	+	+	+	+		+	+	+	+	17	-183.07	405.81	6.05	0.016
+	+	+	+	+	+	+	+	+	+	+	19	-181.71	408.59	8.84	0.004
+	+	+	+		+	+		+			13	-195.36	419.97	20.21	0.000
+	+	+	+		+			+			11	-198.17	420.66	20.90	0.000
+	+		+		+			+			10	-199.39	420.68	20.92	0.000
+	+		+	+			+				10	-200.27	422.45	22.69	0.000
+	+	+	+	+	+	+		+			14	-195.34	422.47	22.71	0.000
+	+	+	+	+			+				11	-199.33	422.98	23.22	0.000
+	+		+	+	+			+			11	-199.37	423.05	23.29	0.000
+	+	+	+	+	+			+			12	-198.15	423.07	23.31	0.000
+	+	+	+	+		+	+				13	-197.27	423.79	24.03	0.000
+	+	+	+	+	+	+		+	+		15	-195.18	424.72	24.96	0.000
+	+		+	+	+		+				11	-200.25	424.82	25.06	0.000
+	+		+	+	+			+	+		12	-199.20	425.16	25.40	0.000
+	+	+	+	+	+			+	+		13	-197.99	425.23	25.47	0.000
+	+	+	+	+	+		+				12	-199.32	425.40	25.64	0.000
+	+	+	+	+	+	+	+				14	-197.26	426.30	26.54	0.000
+	+		+	+	+		+		+		12	-199.80	426.37	26.61	0.000
+	+	+	+	+	+		+		+		13	-198.87	427.00	27.24	0.000
+	+	+	+	+	+	+	+		+		15	-196.82	427.99	28.23	0.000
+	+	+	+			+					10	-210.23	442.38	42.62	0.000
+	+		+								7	-214.16	443.27	43.51	0.000
+	+	+	+								8	-213.13	443.49	43.73	0.000

FA = Fruit abundance, PO = Plant origin, FD = Forest dependency, HL = Habitat loss,
IL = Invasion level, k = number of parameters in each model, × = interaction

Table S4.4 First 30 models of the model set used for model selection to predict guild-specific changes in frugivore visitation rates, with frugivore guilds divided by degree of frugivory (104 models in total). Inclusion of a predictor in a given model is indicated by a plus sign.

Inter-cept	FA	PO	DOF	HL	IL	DOF × PO	DOF × HL	DOF × IL	HL × IL	DOF × HL × IL	k	logLik	AIC_c	Delta AIC_c	Model weight
+	+		+	+	+		+	+	+	+	16	-215.33	467.64	0.00	0.631
+	+	+	+	+	+		+	+	+	+	17	-214.73	469.13	1.49	0.299
+	+		+	+	+		+	+			13	-222.44	474.12	6.48	0.025
+	+	+	+	+	+	+	+	+	+	+	19	-214.67	474.52	6.88	0.020
+	+	+	+	+	+		+	+			14	-221.93	475.65	8.00	0.012
+	+		+	+	+		+	+	+		14	-222.26	476.31	8.66	0.008
+	+	+	+	+	+		+	+	+		15	-221.76	477.88	10.23	0.004
+	+	+	+	+	+	+	+	+			16	-221.92	480.83	13.19	0.001
+	+	+	+	+	+	+	+	+	+		17	-221.75	483.16	15.52	0.000
+	+		+	+			+				10	-231.63	485.18	17.53	0.000
+	+	+	+	+			+				11	-231.09	486.50	18.86	0.000
+	+		+	+	+		+				11	-231.62	487.55	19.90	0.000
+	+	+	+	+	+		+				12	-231.08	488.91	21.27	0.000
+	+		+		+			+			10	-233.68	489.27	21.63	0.000
+	+		+	+	+		+		+		12	-231.28	489.32	21.68	0.000
+	+	+	+		+			+			11	-233.12	490.55	22.91	0.000
+	+	+	+	+	+		+		+		13	-230.75	490.74	23.10	0.000
+	+	+	+	+		+	+				13	-231.06	491.38	23.73	0.000
+	+		+	+	+			+			11	-233.66	491.64	24.00	0.000
+	+	+	+	+	+			+			12	-233.10	492.96	25.32	0.000
+	+		+	+	+			+	+		12	-233.48	493.72	26.07	0.000
+	+	+	+	+	+	+	+				14	-231.05	493.88	26.24	0.000
+	+	+	+	+	+			+	+		13	-232.92	495.09	27.44	0.000
+	+	+	+		+	+		+			13	-233.04	495.32	27.68	0.000
+	+	+	+	+	+	+	+		+		15	-230.72	495.80	28.16	0.000
+	+	+	+	+	+	+		+			14	-233.02	497.83	30.18	0.000
+	+	+	+	+	+	+		+	+		15	-232.84	500.04	32.39	0.000
+	+		+								7	-243.98	502.90	35.26	0.000
+	+	+	+								8	-243.37	503.96	36.32	0.000
+	+		+	+							8	-243.89	505.02	37.37	0.000

FA = Fruit abundance, PO = Plant origin, DOF = Degree of frugivory, HL = Habitat loss,
IL = Invasion level, k = number of parameters in each model, × = interaction

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Curriculum Vitae

Die Seite 140 (Lebenslauf) enthält persönliche Daten. Sie ist deshalb nicht Bestandteil der Online-Veröffentlichung.

Erklärung

Hier mit versichere ich, dass ich meine Dissertation mit dem Titel

„Habitat loss and exotic plant invasions disrupt plant–animal mutualisms in a heterogeneous South African landscape"

selbstständig und ohne unerlaubte Hilfe verfasst habe. Ich habe mich keiner als der in ihr angegebenen Quellen oder Hilfsmittel bedient und alle vollständig oder sinngemäß übernommenen Zitate als solche gekennzeichnet. Diese Dissertation wurde in der vorliegenden oder einer ihr ähnlichen Form noch bei keiner anderen in- oder ausländischen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg an der Lahn, Dezember 2013

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Ingo Graß